MODELING THE LINK BETWEEN PREY AVAILABILITY AND DIET: COMMON MURRE - CAPELIN INTERACTION DURING THE BREEDING SEASON

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Modeling the link between prey availability and diet: Common murre - capelin interaction during the breeding season

by

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Abstract

This study explores the relationship between prey availability and predator's diet, using the common murre-capelin interaction as a case study. Data on prey availability and chick's diets were gathered synoptically during the breeding season. They were then integrated into three structurally different models: a standard multi-category logit model, a model derived from functional response theory and a model that is a hybrid between the former two. The impact of spatial variability in prey availability and the non-random searching behavior of the predator on the models' outcomes was assessed by setting scenarios that represent the murre's perception of its prey field. The model chosen as the best descriptor of the prey availability-diet relationship was the one derived from functional response theory. Insights gained from the models, and implications in the context of functional response theory, predator-prey theory and the management of marine systems, and the use of top predators as monitors of the marine environment are discussed.

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Chapter 1

Introduction

Predation is a key determinant of the structure and dynamics of natural communities (Bax 1998). It is the most basic relationship between two species; all animal species depend on consumption to meet their energetic requirements for maintenance, growth and reproduction, and most animal species are consumed by at least one consumer species. The underlying relationship between predators' diet and prey availability is crucial for determining the outcome of predator-prey interactions, and it is in that context where its importance is best seen.

Besides predator-prey dynamics, this Thesis is set within a framework that has received much attention in the ecological literature, the use of top predators as monitors of environmental change.

First, I present basic elements of predator-prey theory, followed by a brief introduction to functional response theory. Then, I present the concepts on which the use of predators, more specifically seabirds, as monitors is based. Finally, I place my study in its setting. In order to do so, I give a brief overview of the dramatic changes that the Northwest Atlantic ecosystem has suffered during the last decades.

Predator-prey dynamics and the functional response

Considering a simple system with one predator and one prey, where N_i and P are the ith

prey and predator densities, respectively, the Lotka-Volterra model describes the predator-prey dynamics as (Begon *et al.* 1996):

$$\frac{dN_i}{dt} = r_i N_i - F_i P$$
$$\frac{dP}{dt} = P(e_i F_i - \delta) \qquad \text{Eq. 1}$$

where r_i is the intrinsic per-capita growth rate of the ith prey, δ is the per-capita death rate of the predator, and e_i is a measure of conversion efficiency (the rate at which the predator converts prey i into predator). The factor in parentheses in the predator's equation is the numerical response: the growth rate of the predator population (Koen-Alonso 2007). The part of the equation that bears information about the relationship between predators' diet and prey density is F_i, the predator's functional response. The functional response of a given predator with respect to a specific prey i (F_i) is the amount of prey i consumed by a unit of predator per unit time. Therefore, it is a double rate with units [prey] [predator]$^{-1}$ [time]$^{-1}$ (Turchin 2003). Note that defining the functional response as the amount of prey consumed per unit of predator allows us to express it in terms of predator abundance (in which case the unit of predator is the individual predator) or biomass (the functional response is expressed as amount of prey consumed per unit of predator's weight, *e.g.* kg of prey per kg of predator per unit time).

The traditional classification of single-species functional responses (Holling 1959) includes three basic types. Type I is a linear increasing function until it reaches an asymptotic value (Figure 1.1.a), Type II is a hyperbolic curve in which prey consumption decelerates monotonically with prey density until it reaches an asymptote (Figure 1.1.b), Type III has a sigmoidal shape; prey consumption accelerates at low prey densities and

decelerates at high prey densities until reaching an asymptotic consumption (Figure 1.1.c). The original functional response used in the Lotka-Volterra model (Lotka, 1920) does not fit in this classification since it is a linear increasing function of prey density with no upper bound (Figure 1.1.d), and has been dubbed Type 0 (*e.g.* Yodzis 1994). The mortality rate that an individual predator inflicts on the prey population (proportion of prey population that an individual predator consumes) differs depending on the functional response of the predator. For a Type I functional response, the per-capita of predator mortality rate is a constant up to a point (which corresponds to the point where the functional response reaches saturation) where it becomes an inversely dependent function of prey density (Figure 1.2.a). For the Type II response, this rate is a monotonic decreasing function of the prey density (Figure 1.2.b). The mortality rate caused by a predator that exhibits a Type III functional response shows an initial increase because of the accelerated consumption rate, but quickly becomes a decreasing function of prey density due to the decelerated consumption rate (Figure 1.2.c). Finally, a predator that has a Type 0 functional response imposes a constant per-capita of predator mortality rate on the prey population, because its consumption rate is directly proportional to prey density (Figure 1.2.d). For a more complete description of single-species functional responses see Jeschke *et al.* (2002) and Table 1 in Gentleman *et al.* (2003).

The single-species functional response describes the rate at which a predator consumes a given prey as a function of that prey availability. However, if the predator consumes more than one prey the consumption rate of each prey will depend on the availability of all possible prey. The function that describes this relationship is the multi-species

functional response. A general expression for the multi-species functional response is (Koen-Alonso 2007):

$$F_i = \frac{C_i}{1 + \sum_{i=1}^{K} h_i C_i} \qquad \text{Eq. 2}$$

where C_i is the capture rate for prey i, *i.e.* the number of prey consumed per unit of searching time, h_k is the handling time of a single prey item by the predator, and the sum in the denominator is over all prey categories.

The way in which the researcher envisions the details of the predator's feeding biology are expressed through the functional form of the capture rate (Yodzis 1994). The functional form relates the state variables to the rate of change of the capture rate. This rate may depend on just the abundance of the focal prey, or on the abundance of multiple prey, or the conjunction of the prey and predator density (thus incorporating the effects of predator interference or facilitation). It may also be appropriate to consider other variables that can affect the predator's consumption rate such as temperature, age and/or condition.

Over the past decade, there has been a heated discussion in the ecological literature as to the nature of predation; prey dependent (the functional response is determined solely by prey density) or ratio dependent (the functional response depends on the ratio of prey population size to predator population size) (Arditi & Ginzburg 1989, Abrams 1994, Gleeson 1994, Akcakaya *et al.* 1995, Abrams & Ginzburg 2000). This debate motivated empirical studies that found support for the prey dependent (*e.g.* Fussmann *et al.* 2005, Piana *et al.* 2006) and for the ratio dependent (*e.g.* Vucetich *et al.* 2002, Schenk *et al.*

2005) models.

Here I treat the relationship between the diet of common murres (*Uria aalge*) breeding on Funk Island and prey availability. The common murre abundance (and hence density) on Funk Island has been stable since the mid 1990s (Davoren & Montevecchi 2003), and therefore ratio dependent models can not be tested since contrasting murre density observations would be needed to detect a signal in the field data that would allow us to discern if the murre's functional response is prey or ratio dependent.

The expression of the prey dependent multi-species functional response is:

$$F_i = \frac{\alpha_i N_i}{1 + \sum_{i=1}^{K} h_i \alpha_i N_i} \qquad \text{Eq. 3}$$

where α_i is the rate of prey consumption per-capita of prey per unit of searching time. It has been termed the 'rate of successful search' by Holling (1965).

Through a simple example, Matthiopoulos *et al.* (in press) show that the same underlying multi-species functional response can generate single-species functional responses with different shapes, depending on prey availability conditions. This indicates that the traditional classification of single-species functional responses, based on the curve's graphical representation, is not appropriate for multi-species functional responses. I follow Koen-Alonso's (2007) rationale for classifying multi-species functional responses. In this framework, the classification is based on the structure of the rate of successful search (α_i). If α_i is equal to a positive constant coefficient ($\alpha_i = a_i$), then the functional response is the Holling multi-species Type II, and is expressed as:

$$F_i = \frac{a_i N_i}{1 + \sum_{i=1}^{K} h_i a_i N_i} \qquad \text{Eq. 4}$$

If α_i is a function of prey density [$\alpha_i = f(N_i)$], then the functional response is Type III. Although other formulations exist, the most common form to represent a Type III is the Holling multi-species functional response. This functional response is obtained if α_i is a function of the form $\alpha_i = a_i N_i^{b_i}$ (with a_i and b_i constant coefficients):

$$F_i = \frac{a_i N_i^{b_i+1}}{1 + \sum_{i=1}^{K} h_i a_i N_i^{b_i+1}} = \frac{a_i N_i^{\lambda_i}}{1 + \sum_{i=1}^{K} h_i a_i N_i^{\lambda_i}} \qquad \text{Eq. 5}$$

This is a generalized form of the Holling multi-species functional response since both Type II and Type III can be obtained depending on the value of the parameter b_i. If $b_i = 0$ (*i.e.* λ_i=1), then α_i is independent of prey density and thus the functional response is Type II (Eq. 4), otherwise α_i is a function of prey density and the functional response is Type III. In particular, if $b_i = 1$ (*i.e.* λ_i=2) then the functional response is a standard Type III.

As can be seen from the Lotka-Volterra model (Eq. 1), the functional response is a fundamental structural feature of predator-prey models. Therefore, when we develop trophodynamic models the choice of which form of the functional response we use is not a trivial one. Different forms of the functional response lead to dissimilar dynamics, and therefore outcomes of the predator-prey interaction (Yodzis 1994).

Furthermore, it is not only in the domain of pure science where the importance of the functional response is stressed, it also plays an important role in applied science. Trophodynamic models are essential tools for the development and implementation of the

Ecosystem Approach to Fisheries (EAF), an approach that the Government of Canada, and organizations such as ICES (International Council for the Exploration of the Sea) and NAFO (Northwest Atlantic Fisheries Organization) have committed to take.

All this said, it is surprising that assessments of the functional response in natural settings are not more widespread. Before discussing the reasons why there are so few studies of functional responses of predators in their natural environment, it is important to present the notion that the functional response depends on the spatial and temporal scales at which it is measured. Ives *et al.* (1999) distinguish between a 'behavioral functional response' and a 'population functional response'. The former is the per-capita predation rate of a single individual living in a small homogenous area. The latter represents the average per-capita predation rate of predators occupying a complex environment with a heterogeneous prey distribution. In order to measure the 'behavioral functional response', the researcher should be able to follow an individual predator's activities during a period of time and tally the amount of prey the predator consumes. Thus 'cage experiments' measure the 'behavioral functional response' (*e.g.* Holling 1966, Akre & Johnson 1979, Colton 1987, Reeve 1997). In order to estimate the 'population functional response', one must estimate the density of prey (and predator density, if one wishes to include its effects in the model) and the number of prey killed at a relevant time interval. Even if the researcher assumes that the populations are closed (therefore, neglecting the effects of individual movements in and out of the study area), he is faced with the difficult task of measuring the densities of all the relevant prey species. This approach has been taken in a simple predator-prey, semi-closed system (Vucetich *et al.* 2002). An alternative way to fit

a 'population functional response' model is to use the functional response as a structural element of a population dynamics model, and fit this model to a time series (*e.g.* Koen-Alonso & Yodzis 2005a). This approach requires long-term datasets of biomass (or abundance) for all the species of interest, at spatial scales relevant to the predator's feeding biology. The amount and quality of data available are major constraints for the development of multi-species models, although this approach allows for the use of data from different sources, provided that they are standardized prior to their use.

Typically, food web models are formulated at scales that integrate individual responses over time, space and population structure (Koen-Alonso & Yodzis 2005b). Therefore, we should focus on the 'population functional response' for trophodynamic models of natural communities.

By definition, the functional response is the rate of consumption of a predator. Therefore, in order to fit a functional response model one would need to measure this rate in the field, concurrently with prey availability. Recording rates of prey consumption by the common murre is not possible since (for the 'population functional response') that would imply recording the population average number of each prey consumed per unit time and the average allocation of time the common murre makes (the use of loggers may prove useful in this last aspect). Given these exigent data requirements, I do not fit a functional response model in this Thesis. In this study I counted with information on prey availability and the common murre's diet. Therefore, I fit and compare three diet models (these relate a predator's diet to prey availability) with different structure and based on different principles. If the same patterns are found using different approaches, one is

ensured that the answers obtained are robust and that the patterns respond to natural mechanisms and are not an artifact of the modeling exercise. One of the models used was derived from and its parameters are a subset of a functional response model, therefore it allows me to circumvent many of the difficulties previously described and still provide a description of the common murre's functional response.

Seabirds as monitors of environmental change

Top predators integrate ecosystem dynamics at large spatial and temporal scales and they are, therefore, sometimes used as ecosystem indicators. More specifically, seabirds have been considered as monitors of the marine environment due to their abundance, wide ranges, conspicuousness and relative logistical ease of measurement (Boyd *et al.* 2006). They have been used as monitors of such diverse aspects as habitat quality, contaminants, fish stock status, fish biology, changes in marine communities, weather forecasting and climate change (Furness *et al.* 1993). Particular attention has been directed at predators' diets, because this variable is expected to track changes in community structure under the assumption that variations in prey availability are reflected, and most importantly can be effectively detected, in the composition of the diet. Changes in diets have been shown to reflect changes in the predator's prey base, as measured from scientific surveys and commercial fishing operations. For example, in the Barents Sea the proportions of herring (*Clupea harengus*), capelin (*Mallotus villosus*) and juvenile cod (*Gadus morhua*) in the diet of Atlantic puffins (*Fratecula arctica*) showed a strong correlation with abundance estimates derived from standard scientific surveys and so did the proportions of juvenile

herring in the diets of common murres during a 20-year period (Barrett 2002). In the Bering Sea, the abundance of juvenile walleye Pollock (*Theragra chalcogramma*) as well as the proportion of this fish in the diets of Black-legged and red legged kittiwakes (*Rissa tridactyla* and *R. brevirostris*) and common and thick-billed murre (*Uria lomvia*) declined from the 1970s to the 1980s (Hunt *et al.* 1996). As examples of seabirds diets reflecting changes in commercial landings, in the Gulf of California the proportion of sardine (*Sardinops sagax caeruleus*) and anchovy (*Engraulis mordax*) in the diets of the Heermann's gull (*Larus heermanni*) and the elegant tern (*Sterna elegans*) correlate strongly with fisheries landings (Velarde *et al.* 1994). The proportions of prey in the diets of two species of gannets reflect fisheries landings, the Australasian gannet (*Morus serrator*) in southeastern Australia (Bunce 2004), and the Northern gannet in the Northwest Atlantic (Montevecchi & Myers 1995). The commonality among all these studies is that they base their conclusions on correlation analyses; none provide a mechanistic insight into the processes that relate prey availability to predator's diet. This type of mechanistic knowledge could be of great value because it would allow the development of some level of quantitative predictive power, and hence would open the door for using predator's diets as (relative) indices of fish abundance. However, when estimating prey availability from observations of a predator's diet, one must be aware that the functions involved in this inference are not linear and that several sources of uncertainty act simultaneously (Asseburg *et al.* 2006). Therefore, these issues must be considered when predators' diets are intended to be used as monitoring tools.

In the study area, the common murre's has been shown to indicate changes in the

composition of the capelin population (Davoren & Montevecchi 2003).

Northwest Atlantic Ecosystem

The Northwest Atlantic Ecosystem is a sub-Arctic system whose dynamics are strongly influenced by the cold Labrador Current. It is a productive ecosystem that has sustained commercial fisheries for over half a millennium. Once dominated by Atlantic cod, the community experienced dramatic changes during the 1970s and 1980s due to the joint effects of overfishing and ocean climate change (Rice 2002). The cod stock off the Newfoundland shelf collapsed during the early 1990s. The collapse has been attributed to overfishing (Hutchings & Myers 1994), although climate effects have played a role too (Rose *et al.* 2000). During the late1980s and early 1990s the water temperature was the coldest in 40 years, reaching a centennially significant peak in 1991 (Drinkwater 1996). Concurrently, most commercial and many non-commercial demersal species also declined (Rice 2002, Koen-Alonso *et al.* 2006). At the same time as the teleost groundfish stocks declined, some shellfish species increased in abundance, most notably northern shrimp (*Pandalus borealis*) (Lilly *et al.* 2000) and snow crab (*Chionocetes opilio*) (Worm & Myers 2003). There has also been a dramatic increase in the harp seal (*Pagophilus groenlandicus*) population, which grew from 1.8 million individuals in the mid 1970s to *circa* 5.5 millions in the mid 1990s, and has remained at high levels since then (Healey & Stenson 2000). Like seals and invertebrates, many seabird populations have increased in the last twenty years, some dramatically such as northern gannets (*Sula bassana*)(Chardine 2000) and razorbills (*Alca torda*) (Robertson *et al.* 2004, Robertson & Elliot 2002). Common murres are showing a mix of patterns, apparently reduced in the

Gannet Islands, Labrador (Robertson & Elliot 2002), stable in Funk Island (Chardine *et al.* 2003) and increased in the Witless Bay Islands Ecological Reserve (Robertson *et al.* 2004) and in the Cape St. Mary's Ecological Reserve (Regular *et al., in prep.*). Not only have seabird numbers changed, they also bred later and changed diets and foraging strategies during the 1990s, mostly due to changes in capelin biology (Carscadden *et al.* 2002). The diets of northern gannets showed a multi-decadal shift from warm- to cold-water prey (Montevecchi *et al.* 2006), a trend that has reversed in the last two years (Montevecchi *in press*). Common murres in Funk Island delayed breeding two years after the cold-water event in 1991, and delivered smaller and lower quality capelin to their chicks (Davoren & Montevecchi 2003).

Thesis Objectives

Despite the central role that the relationship between predators' diets and prey availability plays in predator-prey dynamics, concurrent field evaluations of these two variables are scarce, mostly due to the difficulty in studying free-ranging predators in the field. These difficulties are heightened when working in a marine environment because the predators act underwater. On the other hand, they are somewhat lessened when studying conspicuous predators such as seabirds, particularly during the breeding season when they must return to the colony to feed their chicks. Several studies have addressed, to differing extents, the relationship between seabirds' diets and prey availability (*e.g.* Montevecchi & Myers 1995, Bost *et al.* 2002, Davoren & Montevecchi 2003, Grémillet *et al.* 2004), but there is still a lack of quantitative assessment of the effect that prey

availability has on diet composition. The general objective of this MSc Thesis is to tackle this issue using common murres as a case study. The particular objectives are:

i. to detect, using quantitative models, the relationship between prey availability and the diet of common murres breeding on Funk Island.

ii. to determine the functional form of the relationship.

In Chapter 2 I analyze prey availability and parental prey deliveries data synoptically, establish that the common murre doesn't take its prey in a direct proportion to availability, and discuss these results in the context of Central place foraging theory (Orians & Pearson 1979).

Chapter 3 is a description of the conceptual approach and implementation of the models relating prey availability to diet.

The models used in this Thesis assume that prey are homogenously distributed and that the murres make use of all their foraging range. These assumptions are not only unrealistic but also are in conflict with our knowledge of the foraging strategies employed by the common murre during the breeding season. Therefore, Chapter 4 explores the effect that the spatial variability in prey availability and the non-random searching behavior of the common murre have on the models' performances and select two representations of the prey field that are the best descriptions of the common murre's perception.

In Chapter 5 I present the results of the modeling exercise, and finally in Chapter 6 I present a synthetic discussion of the Thesis.

Figures

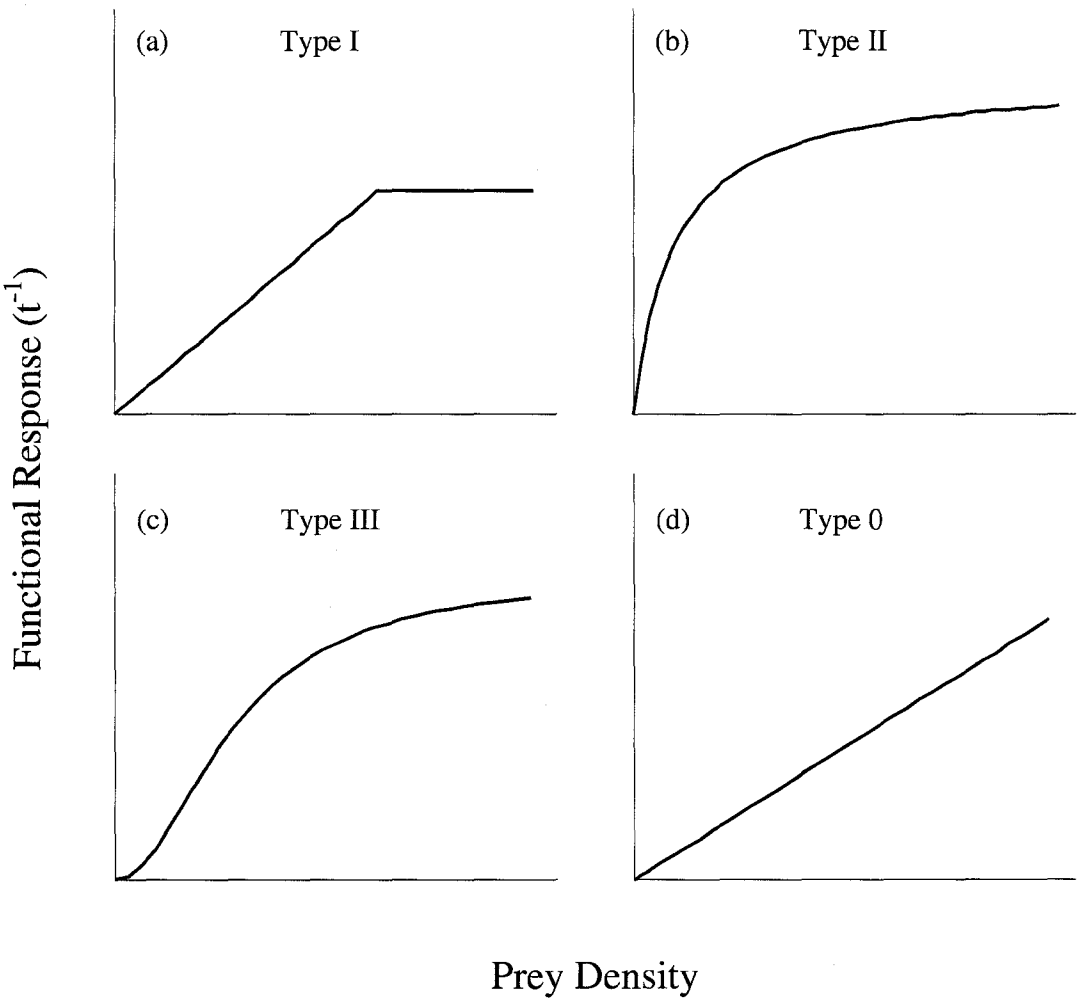


Figure 1.1. Single-species functional response models. (a) Type I, (b) Type II, (c) Type III, (d) Type 0.

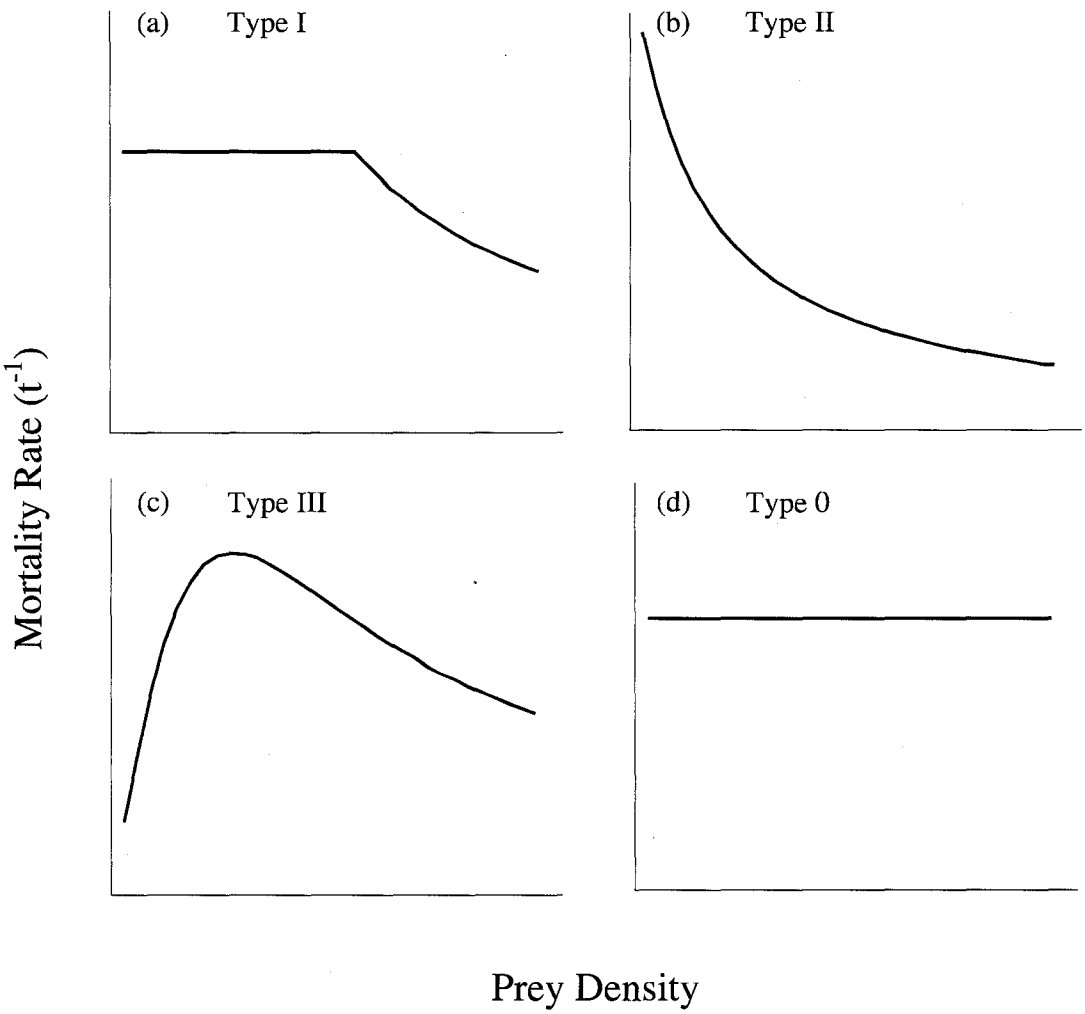


Figure 1.2. Per-capita of predator mortality rate caused by functional responses (a) Type I, (b) Type II, (c) Type III and (d) Type 0.

Chapter 2

Common murre's diet and prey availability

Introduction

During the breeding season, parental seabirds must capture prey and return with them to the colony where they are fed to the offspring. This form of provisioning is known as Central Place Foraging (Orians & Pearson 1979), and its theory is based on the same principles as Foraging Theory (Stephens & Krebs 1986) in that it assumes that a forager increases its fitness by maximizing the net rate of energy delivery to the central place (colony). Central place foraging imposes substantial energetic demands, since a large amount of energy is expended during a round trip. This is especially true for common murres because their flying ability is limited as a result of a wing design that is a compromise between aerial flight and underwater wing-propelled diving (Pennycuick 1987). Normally, in each trip, parental murres bring back a single fish to their chicks (a single-prey loading; Orians & Pearson 1979, Lessells & Stephens 1983) making about 4 foraging trips per day (Birkhead & Nettleship 1987), shared by both parents (Verspoor *et al.* 1987, Burger & Piatt 1990).

Ten species of seabirds breed on Funk Island, an 800 x 400 m granite rock located 60 km off the north-east coast of Newfoundland (Montevecchi & Tuck 1987, WA Montevecchi, *pers. comm.*). The most abundant is the common murre with a population estimate of about 400,000 breeding pairs (Chardine *et al.* 2003).

The common murre is the largest of the living Alcidae, it has a circumpolar distribution, and is one of the most numerous seabirds in the Northern Hemisphere (Ainley *et al.* 2002). It is a pursuit-diving seabird that consumes mainly fish during the breeding season. In the Northwest Atlantic ecosystem, it is the primary seabird consumer of capelin (Montevecchi 2000). Common murres breeding on the Funk Island Seabird Ecological Reserve (the largest colony in the world) feed themselves and their chicks almost exclusively on large, gravid capelin (Davoren & Montevecchi 2003), which they take in hotspots (persistent aggregations of capelin; Davoren *et al.* 2003a, 2003b) around the Reserve. Several aspects of the murre–capelin interaction in the Newfoundland area have been studied, such as the allocation of time and energy by breeding common murres (Burger & Piatt 1990, Cairns *et al.* 1990), the aggregative response of common murres to capelin (Piatt 1990), prey searching behavior (Davoren *et al.* 2003a), the spatial scales at which common murres track capelin aggregations (Davoren *et al.* 2003c), the influence of conspecific's behavior on the choice of foraging habitat (Davoren *et al.* 2003c), and the influence of changes in capelin biology on provisioning of the young (Davoren & Montevecchi 2003).

Capelin is a small, short-lived pelagic schooling fish with a circumpolar distribution in Arctic and sub-Arctic regions (Vilhjálmsson 1994). In Newfoundland, capelin is the dominant forage fish and acts as a link between zooplankton and large vertebrates (*i.e.* marine birds, mammals and large fish; Lavigne 1996). At the same time as the changes in the Northwest Atlantic described in Chapter 1 occurred, capelin also exhibited changes in its biology and ecology: they spawned later in the season and at a younger age and

smaller size (Frank *et al.* 1996, Carscadden & Nakashima 1997). Along with these changes in capelin biology, there was a major reduction in acoustic offshore abundance estimates, although it remains controversial if this reduction actually implied an overall population decline (DFO 2001).

If one is to assess the relationship between prey availability and diet, one must determine if the predator takes its prey in a direct proportion to their availability. Thus, the objective of this Chapter is to describe common murre's diet during the breeding season and compare it to the available prey field around Funk Island.

Material and Methods

Study area

This study was carried out on and around the Funk Island Seabird Ecological Reserve (49°45'N, 53°11'W, Figure 2.1), the world's largest common murre colony (Davoren & Montevecchi 2003).

Data collection

The data used in this Thesis covers the periods 1995-1999 and 2004-2005.

The murre's diet data were collected in the context of Dr. Montevecchi's long-term ecosystem research program and the NSERC Strategic Research Project "The Importance of Capelin (*Mallotus villosus*) Biology in Sustaining Trophic Interactions in the Northwest Atlantic". Diet sampling was undertaken during the breeding season, from late

July to early August. Diet composition was evaluated from parental deliveries to the chicks. Adult murres carrying fish were caught with a pole net and the food loads retrieved from the net. Species, sex and total length were recorded for all prey items.

The prey field within the avian foraging range was characterized using data from two survey programs; the Pelagic Juvenile Fish Surveys conducted by Fisheries and Oceans Canada during the 1990s (Anderson *et al.* 2002) and surveys conducted in the context of the NSERC Strategic Research Project "The Importance of Capelin (*Mallotus villosus*) Biology in Sustaining Trophic Interactions in the Northwest Atlantic" during the 2004 and 2005 summer seasons (Anderson *et al.* 2004). Characteristic positions of the sets made during the 1990s and 2000s surveys are shown in Figure 2.1. Both survey programs were carried out in a systematic fashion, using an IYGPT trawl to sample the upper 60 m of the water column.

Data description

Common murres breeding on Funk Island feed their chicks preferentially on gravid capelin (Davoren & Montevecchi 2003), and rarely catch fish smaller than 100 mm to deliver to their chicks (Birkhead & Nettleship 1987, Barrett 2002, Davoren & Montevecchi 2005). Hence, capelin in the length range consumed by the common murre are dubbed 'suitable capelin', and the term is used hereafter to refer to capelin larger than 100 mm. Three prey categories were defined: small capelin (100-140 mm), large capelin (>140 mm) and other prey (every prey other than capelin). The 140 mm cut-off length was chosen based on capelin life history characteristics. Capelin larger than 140 mm are thought to be 3 years or older (Anderson *et al.* 1999). Typically, capelin mature at 3 or 4

years (Winters 1982), and these groups dominate the spawning population (Carscadden *et al.* 2001a). As an approximation, the two groups of capelin considered can be thought of 'non-spawners' and 'spawners'. Length, instead of maturity classes, were considered because the capelin availability data from the 1990s surveys were not discriminated by maturity. Also, there was a slight temporal mismatch between the diet and prey availability data collection (Table 2.1), and because spawning takes place (changing the status of capelin from 'gravid' to 'spent') in a very short period of time, the availability recorded during the survey would not necessarily reflect the availability when the diet data were being collected.

Diet was characterized in terms of percentage by number $\%N_{ij}$, where *i*: prey category and *j*: year (Hyslop 1980). Bootstrap 95% confidence intervals (CI) were constructed by resampling the observations 50,000 times (Efron & Tibshirani 1993). These CI were used to compare diet composition within years: if in a given year the CI for two prey categories overlap, then the difference in the percentage they contributed in that year to the diet is not significantly different, while it is if the CI do not overlap.

Length frequency distributions were described for the capelin caught in the IYGPT trawl as well as for the capelin delivered by parental murres. These length frequency distributions were compared by year using the Kolmogorov-Smirnov test (Conover 1999). This implies performing multiple comparisons and, in order to maintain the global level of significance of the test (α) at 0.05, the level of significance per comparison (α_c) was corrected according to the Dunn-Šidák method (Sokal & Rohlf 2003). The significance level was $\alpha_c = 1-(1-\alpha)^{1/k}$, where k was the number of intended tests.

For the comparison of the length frequency distributions of capelin delivered by parental murres among years, 21 comparisons (k) were performed and thus α_c was set at 0.0024. In the case of the comparison of the length frequency distributions of capelin delivered by parental murres and caught in the IYGPT trawl, k was 7 and α_c was set at 0.007.

Results

A total of 925 parental deliveries samples were taken over 7 years, with sample sizes per year ranging from 58 to 289 (Table 2.2).

Diet was dominated by capelin in all years. In particular, large capelin dominated the diet in the years when the consumption of small and large capelin was significantly different. The contribution of other prey to the overall diet was almost negligible, with the sole exception of the year 1995 when it accounted for 30% of the diet, being the second most important prey (Figure 2.2).

Most of the capelin consumed were female capelin, with an overall average percentage of 86%. In most years this percentage was greater than 80% and reached a maximum of 97% during 1999 and 2004. The only year when the percentage of female capelin delivered was lower than 80% was 1995 (Table 2.3). This was because a high percentage (32%) of the capelin delivered were classified as 'unknown'; as a result of being too small to make a field determination (most of them were smaller than 120 mm).

The length frequency distribution of capelin delivered by parental common murres was unimodal in all years with the mode located at around 140 mm and individual prey items ranging from 100 to 175 mm (Figure 2.3). Capelin delivered to the chicks had a similar

length frequency distribution through the study period. The only exception was the capelin delivered in 1996; it was significantly different from capelin delivered in all other years (except 1999; Table 2.4). This difference arose because murres delivered slightly larger capelin in 1996 and because the dispersion around the mode was the smallest in that year (Figure 2.3).

A total of 9418 capelin caught in the IYGPT trawl were measured, with sample sizes per year ranging from 600 to 2734 individuals (Table 2.2). Their length ranged from 14 to 185 mm. The length frequency distribution was bimodal (1995, 1996, 1998, 2004 and 2005) or trimodal (1997 and 1999), although some of the modes were very subtle (1996 and 2004). The modes were not consistent between years, ranging from 30 to 140 mm (Figure 2.3). In most years capelin smaller than 100 mm (non-suitable capelin for murres) was abundant, with the exception of the year 2004. Regarding the two categories of suitable capelin, small capelin was more abundant than large capelin throughout the study period, the latter only being considerably abundant during the years 2004 and 1998.

The length frequency distribution of the capelin consumed by common murres was significantly different from the capelin caught in the IYGPT trawl and from the 'suitable' capelin caught in all years (Table 2.5), at the α_c=0.007 level. These differences arose because the common murre does not take capelin in a direct proportion to those available in the environment. They take large capelin to feed their chicks.

Discussion

Common murres breeding on Funk Island deliver almost exclusively capelin to their

chicks. Furthermore, most capelin delivered by parental murres were female. This can be accounted for by the following three plausible, non-mutually exclusive explanations or any combination of them:

i. female availability is higher than male availability due to a sex segregation of capelin schools. There is a sex segregation prior to spawning in capelin. As spawning approaches, two aggregations of capelin are formed: dense, near-bottom schools comprised almost exclusively of males and laxer, midwater schools formed mostly by females (Vilhjálmsson 1994). This segregation renders female capelin availability to the common murre a lot higher than male availability and hence is a likely explanation for the nearly complete absence of male capelin in the murres' diet.

ii. Gravid females might be slower than males and therefore easier to catch. The lower percentage of muscle and the increase in hydrodynamic drag that result from being gravid are likely to reduce female capelin's swimming speed and hence turn them into easier prey than their male conspecifics.

iii. Gravid females have a higher energy density than immature, spent and male capelin (Montevecchi & Piatt 1984) and, therefore, are likely to be selected as prey by parental common murres.

Previous studies (Birkhead & Nettleship 1987, Barrett 2002, Davoren & Montevecchi 2005) have shown that the common murre very rarely takes fish smaller than 100 mm to deliver to its chick. The results of this Chapter not only corroborate this fact, but also show that it does not take 'suitable' capelin in a direct proportion to what is available in

the environment. The modes of the capelin delivered to the chicks were consistently larger than the modes of the 'suitable' capelin available around Funk Island. This observation is in concordance with central place foraging theory (Orians & Pearson 1979) in that the predator does not take every prey it encounters, it only attacks those prey that are more energetically profitable (*i.e.* large capelin). Seen in this context, parental common murres should attempt to maximize their expected delivery rate to the central place, given the energy expenditure in searching and handling prey. Particularly important is the energetic burden that results from traveling to and from the foraging place due to the murre's high wing loading (body mass/wing area; Livezey 1988). Given this high energetic demand, it is expected that parental murres select larger, richer fish to deliver to their offspring.

Throughout this Chapter I have described common murre's parental deliveries and established that diet composition is not directly proportional to prey availability. However, the relationship between diet and prey availability has not yet been addressed. I will do so in the following Chapters.

Tables

Table 2.1. Lag between the last day diet data were collected and the first day of the survey. Note that a negative value of the lag (2005) means that the data collection was contemporaneous.

Year	*Lag*
1995	25
1996	11
1997	3
1998	9
1999	24
2004	6
2005	-3

Table 2.2. Sample sizes of parental deliveries taken and capelin caught in the IYGPT trawl and measured, discriminated by year

Year	*Diet Sample size*	*IYGPT Sample size*
1995	158	623
1996	71	1449
1997	289	600
1998	92	1181
1999	58	1040
2004	153	1791
2005	104	2734
Total	925	9418

Table 2.3. Percentage of capelin delivered by parental murres, discriminated by sex

year	*female*	*male*	*unknown*
1995	60	8	32
1996	96	1	3
1997	87	8	6
1998	85	4	11
1999	97	0	3
2004	97	1	2
2005	96	3	1

Table 2.4. Results of the Kolmogorov-Smirnov test for comparing the length frequency distribution of capelin delivered by parental common murres by year. *: significant at the α_c=0.0024 level of significance.

p/D	1995	1996	1997	1998	1999	2004	2005
1995		0.46	0.11	0.068	0.25	0.14	0.23
1996	2×10^{-8}*		0.37	0.48	0.24	0.41	0.29
1997	0.26	6×10^{-7}*		0.13	0.18	0.07	0.14
1998	0.98	3×10^{-8}*	0.19		0.25	0.1	0.22
1999	0.02	0.05	0.11	0.03		0.2	0.08
2004	0.17	2×10^{-7}*	0.71	0.65	0.08		0.15
2005	0.01	0.0017*	0.09	0.02	0.97	0.11	

Table 2.5. Results of the Kolmogorov-Smirnov tests for comparing the length frequency distribution of capelin delivered by parental murres with capelin caught in the IYGPT trawl and 'suitable' capelin. *: significant at the α_c=0.007 level of significance.

Year	Trawl *vs.* diet		'Suitable' capelin *vs.* diet	
	D	p	D	p
1995	0.93	<0.001*	0.92	<0.001*
1996	0.92	<0.001*	0.56	<0.001*
1997	0.76	<0.001*	0.41	<0.001*
1998	0.47	<0.001*	0.29	<0.001*
1999	0.80	<0.001*	0.77	<0.001*
2004	0.23	<0.001*	0.22	<0.001*
2005	0.85	<0.001*	0.68	<0.001*

Figures

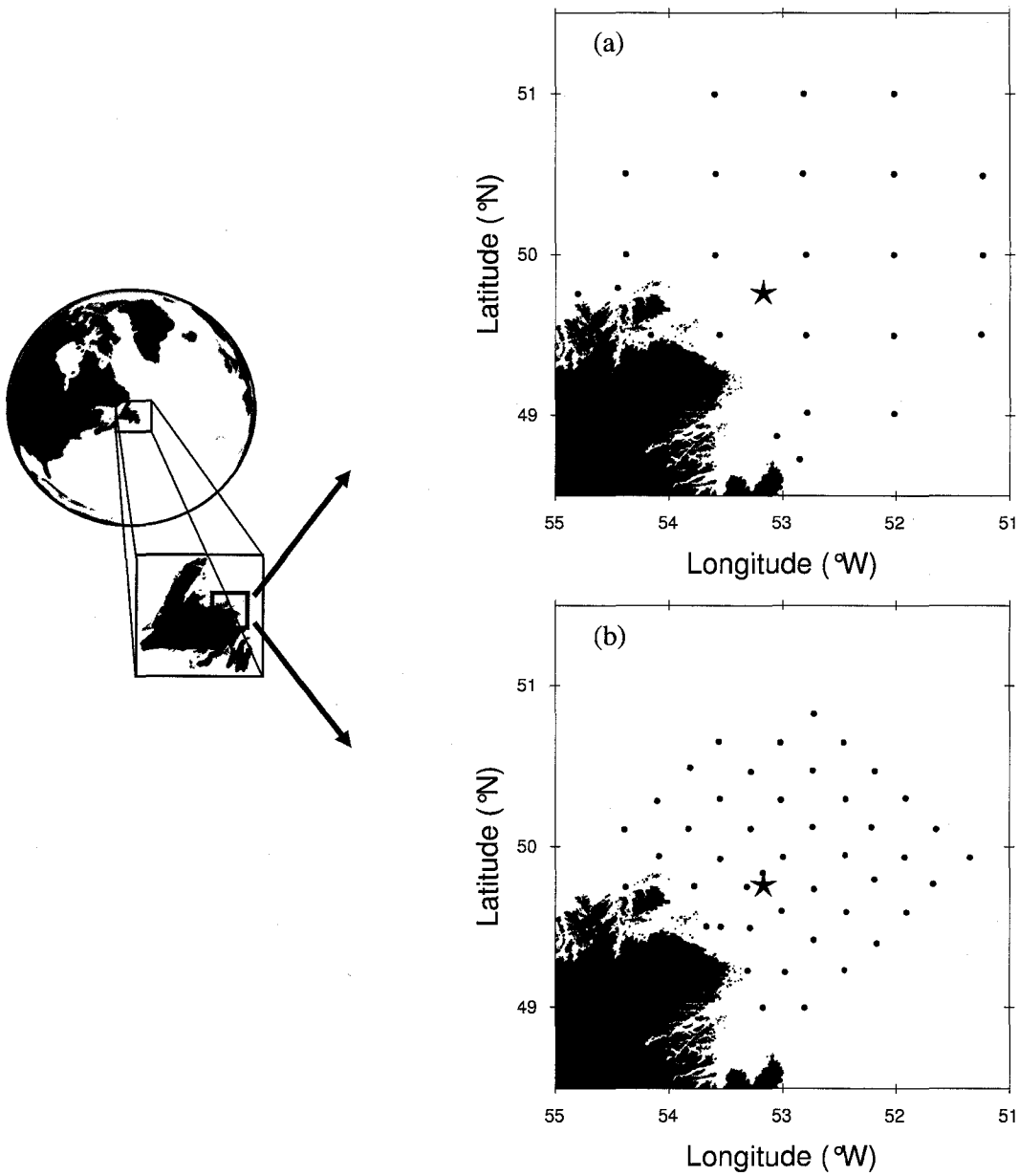


Figure 2.1. Study Area. The star indicates the position of Funk Island and the circles the approximate position of the stations surveyed during (a) 1995-1999 and (b) 2004-2005. The stations shown correspond to the years 1999 and 2004.

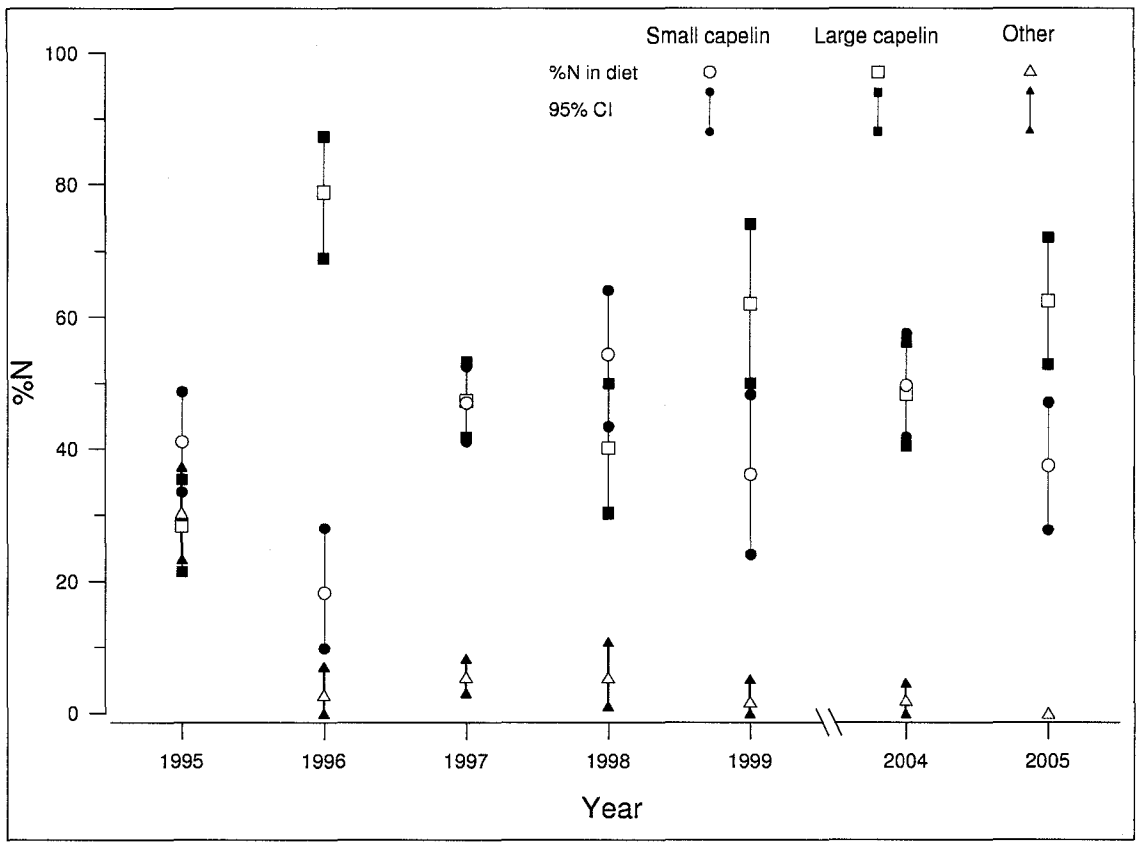


Figure 2.2. Common murre's diet composition. The open circles, squares and triangles are point estimates of the %N that small capelin (100-140 mm), large capelin (>140 mm) and other prey represent in the common murre's diet, respectively. The bars indicate bootstrap 95% CI.

Figure 2.3. Length frequency distributions of capelin in murres' parental deliveries and in the IYGPT trawl. The vertical dotted line indicates 100 mm (capelin >100 mm is 'suitable capelin')

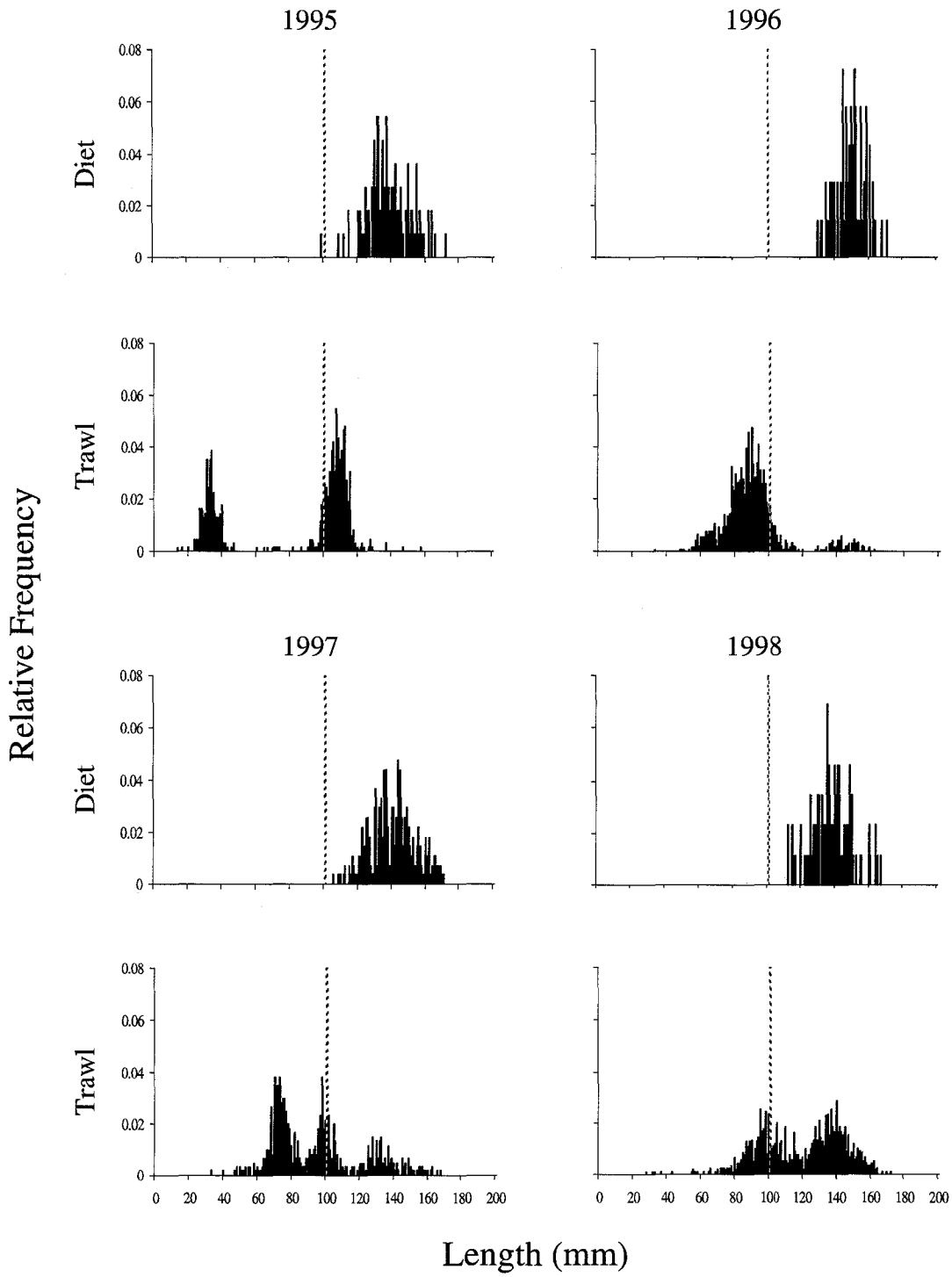
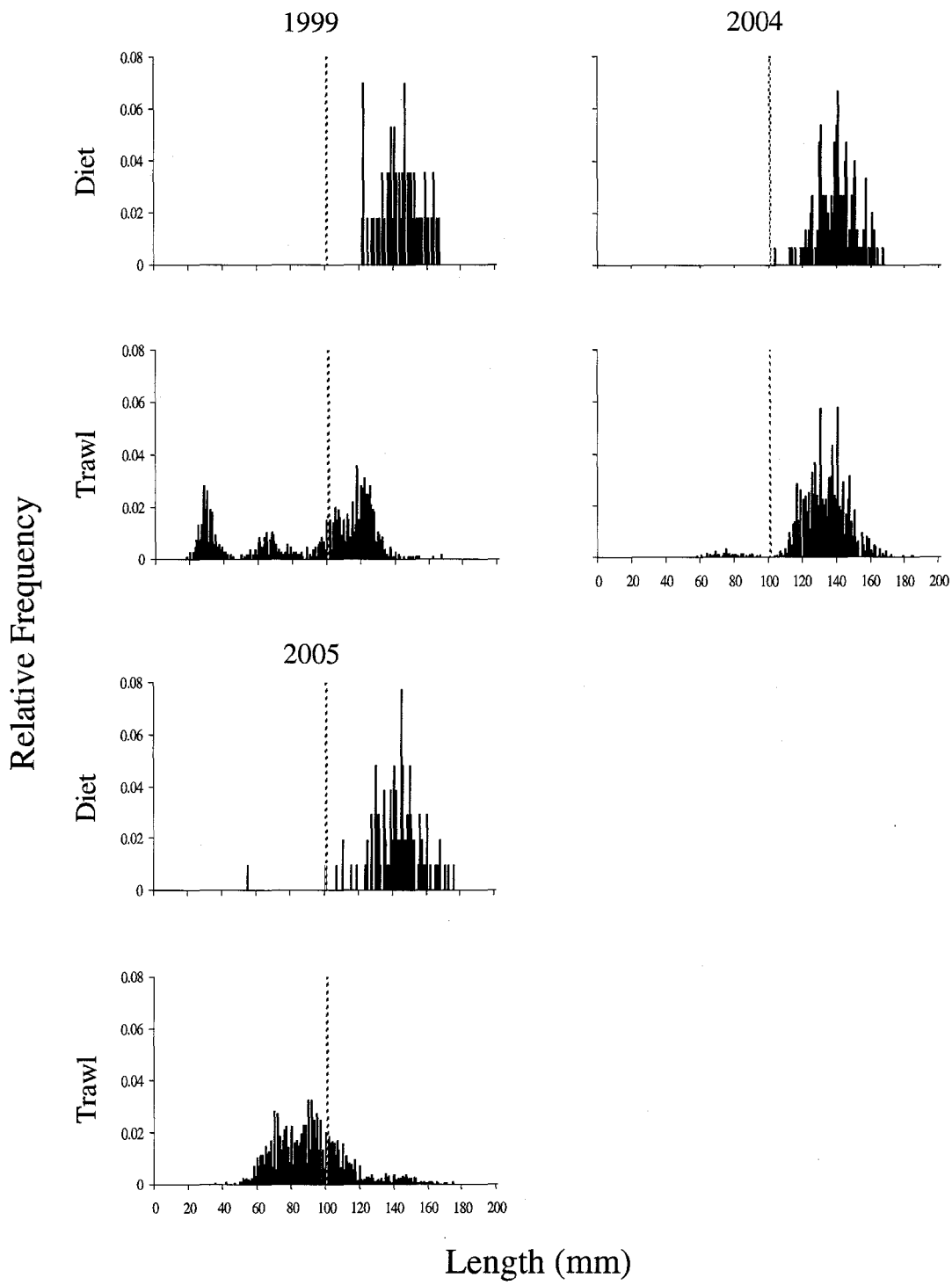

1995
1996
1997
1998
Diet
Trawl
Relative Frequency
0.08
0.06
0.04
0.02
0
0 20 40 60 80 100 120 140 160 180 200
Length (mm)

Figure 2.3. Continued.


1999
2004
2005
Diet
Trawl
Relative Frequency
0.08
0.06
0.04
0.02
0
0 20 40 60 80 100 120 140 160 180 200
Length (mm)

Chapter 3

The models

Introduction

In general, models allow the researcher to synthesize data on individual parts of a system into an integrated view of the system's functioning. In this sense, the models of this Chapter synthesize information on common murre chick's diet and prey availability.

There is clearly a relationship between prey availability and diet. This statement can be proven from extreme cases:

i. assume that only prey *i* is available to a predator, then the predator's diet will be composed solely of prey *i*.

ii. assume that there is no prey *i* available to a predator, then the predator will not consume any prey *i*.

Therefore, asking if the relationship exists bears no intrinsic value. However, two very interesting questions may be posed regarding this issue: 1. given that the relationship exists, can we detect it? More so, are we able to detect it in a natural setting? and 2. what is the functional form of this relationship?

When trying to detect the relationship between prey availability and diet we are not concerned with the extreme cases I described above, rather we are interested in the cases that lie between these extremes. A sound starting point for evaluating this relationship is the predator's functional response since it quantifies the amount of prey consumed.

Although there are a few studies that evaluate predator's functional responses, most of them are carried out in laboratory settings and with insect predators (*e.g.* Holling 1966, Akre & Johnson 1979, Colton 1987, Gismervik & Andersen 1997, Reeve 1997), while field tests are rare, particularly in marine environments. Even fewer studies have looked at a vertebrate predator's functional responses in unmanipulated field settings, for example, Messier (1994), Vucetich *et al.* (2002), Middlemas *et al.* (2005), Asseburg (2006), Asseburg *et al.* (2006) and Smout & Lindstrøm (2007).

Not only the logistical difficulties associated with fitting these kind of models (see Chapter 1) have prevented researchers from trying to establish a quantitative link between diet and prey availability, but also the widespread perception that endeavors of this nature are not cost-effective, given that the signal-to-noise ratio of ecological data is typically low.

Although they are a natural starting point, functional response models are not the only way to quantitatively relate diet to prey availability. Logit models, despite not being based on ecological or behavioral considerations, can be applied to assess the effect of prey density on a predator's diet (*e.g.* Peltonen *et al.* 1996). These models belong to the generalized linear models family (McCullagh & Nelder 1989) and, in the case of diet modeling, predict the predator's diet composition from prey availability and/or other continuous or categorical variables.

Why is the functional form of the relationship important?

The functional form of the relationship between diet and prey availability is of great

interest from both, pure and applied science perspectives (Yodzis 1994). It is of interest scientifically because it represents the researcher's view of how the predation process itself occurs and what factors affect it. For instance, one might formulate a relationship that is only prey density dependent and the density of the predator plays no role or one could choose to incorporate the effects of predator interference or facilitation.

Furthermore, depending on how the researcher envisions the biological details of the process he can specify if the relationship depends only on the density of one prey species or on the densities of all or a handful or prey species.

From an applied science perspective, it is important because it can have a profound effect on the dynamics and results of multi-species and food web models, which may be called upon to provide management advice in the context of Ecosystem-Based Fisheries Management (Plagányi 2007). In a simple thought experiment (*gedankenexperiment*), Yodzis (1994) showed the effects of assuming different forms of a predator's functional response in an exploited system. He modeled a system with a predator population (*e.g.* marine mammal) and a prey population (*e.g.* fish), where the prey population is harvested and showed how assuming different forms of the functional response dramatically affects not only both species' population dynamics but also fisheries yields. Taking this experience to a real-life situation, Koen-Alonso & Yodzis (2005a) modeled a system with three prey populations and one predator population, where the three prey are commercially exploited and the predator was exploited in the past. The model's ability to capture the time series depended to a large extent on which of the five different formulations of the functional response was being used. More importantly from a

management perspective, these authors found that the use of different functional responses led to very different population responses to exploitation.

All of this highlights the importance of carefully scrutinizing the functional form of the relationship between prey availability and diet.

In this Chapter I describe the methodology I used to tackle the questions: can we detect a relationship between prey availability and a vertebrate predator's diet in an unmanipulated a field setting?, and what is the functional form of this relationship?

Methods

In this section I describe the general approach taken to calculate the probabilities of consuming an individual of a given prey category (consider parental deliveries as realizations of a multinomial distribution) and introduce the models used to relate diet to prey availability. One of them, the statistical model, belongs to a family of models that have been successfully used before (*e.g.* Peltonen *et al.* 1996), while the other two (to the best of my knowledge) have not been implemented before. The ecological model is based on functional response theory and the hybrid model shares features of the other two. This allows me to evaluate the performance of a new model based on ecological theory compared to a model that has been used in the past but has no ecological foundation and to a model that represents a midpoint between the former two.

Diet composition as a multinomial distribution

I considered each observed parental delivery as a multinomial random variable $\mathbf{Y}_j = \{y_{j,sc}, y_{j,lc}, y_{j,ot}\}$ where each y_{ji} is the number of individuals of the *i*th prey category observed in the *j*th individual bird, *sc* is small capelin, *lc* is large capelin and *ot* is other prey. The common murre being a single-prey loader, only one y_{ji} per parental delivery $\mathbf{Y}_j$ had a non-zero value.

Under the multinomial distribution, the probability of a particular observation is given by

$$\Pr[\mathbf{Y}_j = \{y_{j,sc}, y_{j,lc}, y_{j,ot}\}] = \frac{n_j!}{y_{j,sc}!\,y_{j,lc}!\,y_{j,ot}!}\,\pi_{sc}^{y_{j,sc}}\,\pi_{lc}^{y_{j,lc}}\,\pi_{ot}^{y_{j,ot}} \qquad \text{Eq. 6}$$

where n_j is the number of parental deliveries observed, and π_i is the probability of feeding on the *i*th prey category subject to the constraint that $\sum_{i=sc,lc,ot} \pi_i = 1$ (Gelman *et al.* 2004).

Hence, the multinomial log-likelihood is expressed as

$$\ln[\mathscr{L}(\boldsymbol{\theta})] = \sum_{j=1}^{N}\left[\ln\left(\frac{n_j!}{y_{j,sc}!\,y_{j,lc}!\,y_{j,ot}!}\right) + \sum_{i=sc,lc,ot} y_{j,i}\ln\pi_i\right] \qquad \text{Eq. 7}$$

where N is the number of observed parental deliveries.

The models

Statistical model

The statistical model is a multi-category logit model. These are generalized linear models

that are used for discrete-choice modeling of a subject's choice from one of several options (Agresti 2002).

In all logit models the expression of the probability of a response i is of the form:

$$\pi_i = \frac{\exp[\eta_i]}{\sum_{i=1}^{K} \exp[\eta_i]} \qquad \text{Eq. 8}$$

where η_i is a linear predictor. In the context of generalized linear models, a linear predictor is the systematic component of the model that relates the data's expected value to a linear combination of variables of interest (X_i) (McCullagh & Nelder 1989):

$$\eta_i = \sum_m \beta_m X_m \qquad \text{Eq. 9}$$

Throughout this Thesis I use the term 'linear predictor' to refer to the systematic components of not only the statistical models, but of all the models I present.

In order to prevent confusions with the use of subscripts, I point out the fact that in this Thesis I estimate the probability of consuming a given prey (i = *sc, lc, ot*) as a function of the density of those prey (m = *sc, lc, ot*). Hence, when I use the subscript 'i' it refers to the prey category for which I'm estimating the probability of being consumed (the response variable) and when I use the subscript 'm' I refer to the prey category whose density is used as an explanatory variable.

Expressing the linear predictor as a function of prey densities, the probability of a parental murre delivering a prey i (π_i) is:

$$\pi_{i=} \frac{\exp\left[\beta_{0i} + \sum_{m=sc,lc,ot} \beta_{m,i} N_m\right]}{\sum_{k=sc,lc,ot} \exp\left[\beta_{0k} + \sum_{m=sc,lc,ot} \beta_{m,k} N_m\right]} \qquad \text{Eq. 10}$$

where N_m is the density of the mth prey. The model parameters $\beta_{m,i}$ can be interpreted as the effect that the density of the mth prey category has on the log odds of consuming a prey item of the ith prey category.

Note that the linear predictor for the ith prey is a linear function of all prey densities.

Ecological model

For the ecological approach I based the model on the generalized Holling formulation of the multi-species functional response (Eq. 5). Considering the prey categories described in the previous Chapter, the expression of the functional response is:

$$F_i = \frac{a_i N_i^{\lambda_i}}{1 + \sum_{k=sc,lc,ot} h_k a_k N_k^{\lambda_k}} \qquad \text{Eq. 11}$$

Considering that the functional response is a consumption rate, we can define the proportion of the ith prey category in the diet as:

$$p_i = \frac{F_i}{\sum_{k=sc,lc,ot} F_k} = \frac{a_i N_i^{\lambda_i}}{\sum_{k=sc,lc,ot} a_k N_k^{\lambda_k}} \qquad \text{Eq. 12}$$

This proportion can be used as an estimator of the probability of consuming an item of the *i*th prey category (*i.e.* $\hat{\pi}_i = p_i$). Hence, the ecological model for the probability of consuming a given prey is

$$\hat{\pi}_i = \frac{a_i N_i^{\lambda_i}}{\sum_{k=sc,lc,ot} a_k N_k^{\lambda_k}} \qquad \text{Eq. 13}$$

Note that the proportion of the *i*th prey category in the diet is independent of handling time (h_i). Therefore, its estimation does not imply the logistical difficulties imposed by the estimation of rates in the field.

The model presented in Eq. 13 was fitted to the diet data. Next, I present an algebraic derivation that explicitly presents features of this model that can be compared to those of the statistical model, and that leads to the derivation of the third model used in this Thesis, the hybrid model.

The ecological model (Eq. 13) can be rewritten in the form of a logit model (Eq. 8); by redefining:

$$A_i = \ln(a_i) \qquad \text{Eq. 14}$$

then, $a_i = \exp(A_i)$

$$\gamma_i = \lambda_i \qquad \text{Eq. 15}$$

then, $N_i^{\lambda_i} = \exp[\gamma_i \ln(N_i)]$

Now, putting the two equations together, the expression of the linear predictor for the *i*th

prey is

$$a_i N_i^{\lambda_i} = \exp[A_i + \gamma_i \ln(N_i)] \qquad \text{Eq. 16}$$

Substituting Eq. 16 into Eq. 13, the ecological model may be written as:

$$\hat{\pi}_i = \frac{\exp[A_i + \gamma_i \ln(N_i)]}{\sum_{k=sc,lc,ot} \exp[A_k + \gamma_k \ln(N_k)]} \qquad \text{Eq. 17}$$

Note that the linear predictor (Eq. 16) is a function of only the *i*th prey density, and that this density is in a logarithmic scale.

Hybrid model

The model I describe in this section has the form of a logit model (Eq. 8), and its linear predictor combines features of the linear predictors of the statistical and ecological model, hence the name 'hybrid'. So far, I have described the linear predictors in terms of being either a function solely of the density of the *i*th prey or a function of all prey densities, and in terms of the scale in which prey density is expressed (*i.e.* linear or logarithmic). In order to build this model, the linear predictor for the *i*th prey was expressed as a function of all prey densities in a logarithmic scale. The logarithmic scale is appropriate to describe capelin density since, as most short-lived pelagic fish, it shows a large interannual variability in abundance and the logarithmic scale is the preferred scale to represent data whose values span a large range.

The expression of the hybrid model is similar to that of Eq. 17 in the sense that its linear predictor is equal to *e* elevated to a constant plus a term that is a function of prey density.

In the case of the hybrid model, the term that is a function of prey density is extended to be a function of all prey densities in a multiplicative fashion (*i.e.*, if written in a linear scale as in Eq. 13, the linear predictor is equal to the product of all prey densities elevated to their corresponding shape parameters). Thus, the hybrid model is:

$$\pi_i = \frac{\exp\left[B_i + \sum_{m=sc,lc,ot} \gamma_{m,i} \ln(N_m)\right]}{\sum_{k=sc,lc,ot} \exp\left[B_k + \sum_{m=sc,lc,ot} \gamma_{m,k} \ln(N_m)\right]} \qquad \text{Eq. 18}$$

Models assumptions

Explicitly stating the assumptions one makes when building a model enables the reader to perform a critical evaluation of the model's adequacy. All the models presented in this Thesis have the below-described built-in assumptions. Further assumptions about prey distribution and predator foraging behavior are detailed and explored in the following Chapter. The assumptions built into the models presented above are:

i. Common murre takes the bulk of its prey in the upper 60 m of the water column.

By virtue of using the IYGPT trawl to describe the prey field, I assume that the common murre takes the bulk of its prey in the upper portion of the water column, even though they can dive up to 180 m (Piatt & Nettleship 1985). This assumption can be justified with empirical support; common murres off Hornøya (Norway) dove to a maximum depth of 37 m, being the mean

maximum dive depth 10.2 ± 7.6m (Tremblay *et al.* 2003). Furthermore, a congeneric species, the thick-billed murre spends most of its time-at-depth between 21 and 40 m despite the fact that its maximum dive depth is 210 m (Croll *et al.* 1992).

ii. Prey availability remained constant from the moment of the diet sampling to the moment of the survey.

The analyses carried out in this Thesis assume that prey availability remained constant from the moment of the diet sampling to the moment of the survey. Even though capelin shows a low post-spawning survival rate (Shackell *et al.* 1994), I assume that prey availability did not change dramatically since in most years the temporal mismatch between the period of diet sampling and the survey was in the order of 10 days or less (Table 2.1). Only in two years (1995 and 1999) the temporal mismatch was higher and of the same magnitude than both the murre chick rearing period (approximately 3 weeks; Ainley *et al.* 2002) and the capelin spawning period (2 to 3 weeks; Leggett *et al.* 1984, Nakashima & Wheeler 2002). However, I don't think this invalidates the assumption since most of the post-spawning capelin was likely still in the study area in staging areas (Davoren *et al.* 2006) or en route to the offshore areas.

Models Implementation

Models were fitted by maximizing the multinomial log-likelihood function.

Multi-category logit models pair each response with a baseline category; thus the log odds for all other categories are calculated relative to the baseline. If the response variable has I (in this case 3; *sc, lc* and *ot*) categories, then $I - 1$ (*i.e.* 2) equations simultaneously describe log odds for all pairs of categories (Agresti 2002). A reference category was also set for fitting the ecological model. This ensures that only one combination of parameter values will maximize the log-likelihood function. If we did not fix any parameter, then multiple combinations of parameters would potentially yield the same value of the likelihood function. Therefore, all parameter values are calculated relative to the reference category. The baseline category is often defined as the last or the most common one. In this study, the most common response category was 'large capelin' (Figure 2.2) and hence was set as baseline. For the statistical and hybrid models, this means that the equations for 'small capelin' and 'other prey' determine the logits for all response categories. In the case of the ecological model, the parameter a_{lc} was set equal to one (1).

The hybrid and multi-category logit models were implemented in SAS Proc Logistic (SAS INSTITUTE 2005) and the ecological model was written in the programming language Fortran 77.

SAS implements a Newton-Raphson algorithm to fit multi-category logit models. This is an iterative method for solving nonlinear equations, whose implementation McCullagh & Nelder (1989) recommend to find the maximum likelihood estimators (MLE) of the parameters of generalized linear models

In the case of the ecological model, the Enhanced Simulated Annealing (ESA) algorithm

(Siarry *et al.* 1997) was implemented. The extremum (maxima or minima) of a function f can be either global (the function's true maximum or minimum value) or local (the extreme value of f in a neighbourhood containing the value). By definition, an MLE is the global maximum of the likelihood function. Hence, we are interested in finding the global maximum of the likelihood function. This task may be cumbersome because optimization algorithms can get 'trapped' in local extrema. This is especially true in multi-dimensional problems where the algorithm must search in a sometimes convoluted parameter space. Simulated annealing methods have proven to be successful in finding global extrema. Although more computationally intensive, these algorithms are able to find a global extremum hidden among many, poorer, local extrema (Press *et al.* 1992).

In order to obtain a measure of the uncertainty in the parameter values, 95% CI were built around them. In the case of the parameters of the statistical and hybrid models, the procedure SAS Proc Logistic calculates 95% Wald confidence limits for the parameters (SAS INSTITUTE 2005). In the case of the ecological model, approximate 95% CI for the parameters were calculated by constructing likelihood profiles for each of them (Hilborn & Mangel 1997). The profiles are constructed based on the likelihood ratio test (LRT). Denote the vector of parameters of the model by $\boldsymbol{\theta}$. The test involves a comparison of the maximum value the likelihood can take when $\boldsymbol{\theta}$ is allowed to take any value in the parameter space, and the maximum value of the likelihood when $\boldsymbol{\theta}$ is restricted by the hypothesis. Denote the model in the former case by $M_{generalized}$, in the latter case by $M_{restricted}$, the data by Y and the negative log-likelihoods of the data, given

the models, by $\ln(\mathscr{L}\{Y \mid M_{generalized}\})$ and $\ln(\mathscr{L}\{Y \mid M_{restricted}\})$. Twice the difference between these log-likelihoods

$$\mathscr{R} = 2\,[\ln(\mathscr{L}\{Y \mid M_{restricted}\}) - \ln(\mathscr{L}\{Y \mid M_{generalized}\})]$$

approximately follows a chi-square distribution, with the degrees of freedom equal to the difference in the number of estimated parameters between models. The chi-square probability represents the probability that the restricted model fits the data equally well as the generalized model. A likelihood profile for a given parameter, say θ_i, is built by varying it systematically and performing a LRT at each value of θ_i. Next, the differences in log-likelihoods and their corresponding p-values as a function of the value of θ_i are plotted. Confidence intervals are then constructed by drawing a horizontal line at the desired level (*e.g.* 95 %) and seeing where the line intersects the χ^2 probability curve.

I have described the tools I used to tackle the two questions that motivated this Thesis: can we detect a relationship between prey availability and a predator's diet?, what is the form of this relationship? But before discussing the model fits, I will describe how I approached the spatial aspect of the prey field. The reader may think of it this way: I will first deal with the independent variable of the models (prey densities), and once that aspect is settled I will move on to the dependent variable (predator's diet). Thus, in Chapter 4 I describe the approach taken to tackle the spatial component of the prey field, in Chapter 5 I present and discuss the model results, and finally I provide a synthetic discussion in Chapter 6.

Chapter 4

The prey field

Introduction

The models I described in the previous Chapter assume that the prey are homogenously distributed and that the murres make use of all their foraging range. Naturally, this assumption is unrealistic since pelagic fish aggregate in shoals. Central-Place Foraging theory (Orians & Pearson 1979) predicts that individuals minimize the duration of round trips in order to maximize the rate of food delivery. Hence, it is likely that during chick rearing seabirds utilize searching tactics to find fish shoals. Davoren *et al.* (2003a) contend that common murres breeding at Funk Island use memory and local enhancement (cueing on conspecifics' foraging activities within visual range) as search tactics in order to locate persistent aggregations of capelin ('hotspots').

Thus, the models' implicit assumption of homogenous distribution of prey and utilization of feeding grounds throughout avian foraging range is not only unrealistic but it also is in conflict with our knowledge of the common murre's foraging behavior.

In this Chapter I will explore the impact that spatial variability in prey availability and the non-random searching behavior of the predator have on the models described in the previous Chapter.

Methods

I set up representations of the common murre's prey field (hereafter called 'scenarios') and selected the most likely ones based on a goodness-of-fit criterion.

The scenarios describe the murre's potential perceptions of its foraging environment. Such perceptions encompass prey abundance and distribution. The extent of the area included in the prey field description was chosen so as to encompass the maximum potential foraging range of breeding common murres (123 km during incubation and 80 km during chick rearing; Cairns *et al.* 1987). Prey densities were estimated using trawl sets selected according to two criteria:

i. high numbers of capelin were caught in a given set.

These sets were chosen to represent dense aggregations of capelin, presumably on which the murres would preferentially feed. On an explanatory note, I dub the scenarios that comply with this rule 'Dense spot' and not 'Hotspot', because the latter is used to refer to areas where high abundance of organisms are spatially concentrated and in particular for the study area, Davoren (2007) reports the existence of a hotspot in the inshore area where capelin demersal spawning takes place and could not be surveyed because it is located in an area too shallow to be accessed with the vessels used to gather the data used in this Thesis.

ii. the set was made inshore of Funk Island.

Davoren *et al.* (2006) report persistent aggregations of capelin shoals off the straight shore of Bonavista Bay, Newfoundland during July due to favourable

habitat conditions for spawning and staging. These aggregations may provide a predictable food source for common murres, hence it is possible that they make a preferential use of the inshore area for foraging.

In order to describe the prey density, I employed the Δ-lognormal estimator, which assumes that the non-zero observations from the survey follow a lognormal distribution (Pennington 1996). This estimator has the advantage of not being overly influenced by an occasional large catch (Pennington & Strømme 1998). This feature is particularly relevant when trying to estimate the abundance of pelagic shoaling fish because a single catch may account for more than half of the total catch of the survey. On the other hand, lognormal-based estimators of abundance are sensitive to departures from lognormality, which can lead to biases in the population mean abundance estimate (Myers & Pepin 1990). Therefore, the non-zero observations from the surveys were checked for deviations from lognormality using the Lilliefors test for normality (Conover 1999) applied to the (log)counts. Multiple comparisons (k = 7) were performed per prey category, and hence the level of significance was adjusted accordingly (see Chapter 2) to α_c = 0.007. When performing multiple comparisons, one controls the Type I error at the expense of a loss of power (Sokal & Rohlf 2003; in this context, power is the probability of detecting a non-lognormally distributed set of observations), which could potentially be a problem for detecting deviations from lognormality. The counts of 'Other prey' followed a lognormal distribution (Table 4.1). In the case of capelin some of the observations clearly followed a lognormal distribution (1995, 1996 and 1998), some did

not follow it (2004 and 2005) and for the rest of the years (1997 and 1999) while the p-values were low, lognormality could not be rejected at the α_c value, although this could result from the loss of power. Given the clear signal in the 'Other prey' data, the mixed signal in the capelin data, and the clear advantages that the Δ-lognormal estimator of abundance has for estimating the abundance of pelagic shoaling fish, I used it to describe the prey field available to the common murre.

Given that capelin length was not recorded in all IYGPT sets, capelin density per size class (*i.e.* small and large) per year was estimated as the product of the Δ-lognormal estimator of abundance times the proportion of capelin of a given size class caught in the IYGPT trawl.

The Scenarios

Each scenario is based on an underlying hypothesis about how common murres utilize their foraging environment and perceive prey aggregations. The names of the scenarios derive from the assumed foraging behavior the common murre shows in each of them. For visualization purposes, I show capelin density contour maps (Figure 4.1) that represent each of the scenarios. The density contours in these maps were created by applying a smoothed kriging to the trawl data.

i. *Random foraging:*

The common murre forages throughout its foraging range, and there is no prey density threshold above which it perceives prey aggregations. The probability of consuming a given prey depends on the availability of prey across all of the murre's foraging range. I estimated prey availability considering all the IYGPT

sets made in the study area (Figure 4.1.a). The average number of sets considered was 31.1 (Table 4.2).

ii. *Inshore foraging*:

The common murre forages only in the area inshore of Funk Island, and there is no prey density threshold above which it perceives prey aggregations. The probability of consuming a given prey depends on the availability of prey in the near shore. I estimated prey availability considering the IYGPT sets made inshore of Funk Island (Figure 4.1.b). The average number of sets considered was 15.4 (Table 4.2).

iii. *Foraging in dense spots:*

The common murre forages throughout its foraging range, and there is a prey density threshold above which it perceives prey aggregations. The probability of consuming a given prey depends on the availability of prey in areas with dense aggregations of capelin. I estimated prey availability considering the IYGPT sets in which a large (>35) number of capelin were caught (Figure 4.1.c). The average number of sets considered was 6.7 (Table 4.2).

iv. *Foraging in dense spots inshore:*

The common murre forages only in the area inshore of Funk Island, and there is a prey density threshold above which it perceives prey aggregations. The probability of consuming a given prey depends on the availability of prey in areas with dense aggregations of capelin in the near shore. I estimated prey availability from the IYGPT sets made inshore of Funk Island and in which a

large (>35) number of capelin was caught (Figure 4.1.d). The average number of sets considered was 4.5 (Table 4.2).

Scenario Selection Criterion

In order to select the best representations of the common murre's prey field, I fitted the three models presented in the previous Chapter considering the four scenarios presented above (yielding a total of 12 combinations of models-scenarios), and chose as the bests those scenarios that provided the best fit for a given model. The Akaike information criterion (AIC) is commonly used for ranking a suite of competing non-nested models and selecting the best among them. This criterion is the main tool of the information-theoretic approach (Burnham & Anderson 2002). However, taking such an approach for selecting the best scenarios would be inappropriate because I call scenarios to different representations of the prey field (*i.e.*, the explanatory variable), while the information-theoretic approach is advocated for ranking fitted models (*i.e.*, it focuses on the response variable). Burnham & Anderson (2002, p. 80) explicitly state that models can be compared using the information criteria only when they have been fitted to exactly the same data set.

Since the selection of the best scenarios (given a model) implies comparing models that have been fit to different subsets of data, it was done according to a χ^2 goodness-of-fit criterion. This measure of goodness-of-fit summarizes the discrepancy between observed values and the values expected under the model in question. The observed values were the proportion of each prey category in the diet by year and their expected values were the probability of consuming those prey estimated by the models. It is worth noting that

the χ^2 measure used is merely descriptive and does not imply hypothesis testing, thus when I refer to a scenario being better than any other I mean that the discrepancy between observations and model predictions is smaller but I do not mean that is significantly better in a statistical sense.

Results

The selection of the best scenarios has to be done on a model-by-model basis, hence in this section I describe for each of the three models which scenarios had the best fit.

In every case, there was one scenario which clearly showed a considerable better fit than the rest. In the case of the statistical model, the Inshore foraging scenario showed the best fit, while the Random foraging scenario performed best for the ecological and hybrid models (Table 4.3).

The prey field in the scenarios Random foraging (Figure 4.2.) and Inshore foraging (Figure 4.3.) share common features. In both scenarios, it can be schematically characterized in terms of the abundance of suitable capelin as being either high or low. In the case of the Random foraging scenario, the high capelin abundance years were 1997, 1998 and 2004, while only in 1997 and 2004 was there high abundance of capelin in the Inshore foraging scenario. Another common feature between these two scenarios was that in most years the most abundant prey were small capelin, with the exception of the year 1995 when other prey was the most abundant prey category and there were almost no large capelin in the study area. Although the pattern in prey availability is the same on both scenarios, the scales in which it is measured differ; in the case of the Random

foraging scenario prey availability ranges from 7.5 to 29,000 fish km^{-2}, while in the Inshore foraging scenario it ranges from 16 to 92,500 fish km^{-2}. One last characteristic shared by the prey field in both scenarios is that both small and large capelin's availabilities are much more variable than the availability of other prey (Table 4.4). The coefficient of variation of Other prey is in the order of 0.5 while that of capelin is larger than 1 in all cases, and it reaches a high of 1.8 for large capelin in the Inshore foraging scenario.

Discussion

The Inshore Foraging and Random foraging scenarios showed the best goodness-of-fit when considering the statistical and ecological and hybrid models, respectively.

Given that the common murres breeding on Funk Island take their prey in hotspots (Davoren *et al.* 2003a), one would have initially expected that the Dense spots scenario would yield the best fit. However, in order to correctly interpret the results of this Chapter we must consider that they are not results from individual behavioral observations, but they represent the way in which the common murre integrates information about its prey field over differing spatial and temporal scales. Hence, they do not contradict Davoren *et al.*'s (2003a) results, but provide a different insight into this seabird's foraging ecology.

The prey fields described by the Inshore Foraging and Random foraging scenarios integrate information on a meso-scale (~ 100 km) and on a temporal scale of around two weeks. I interpret the results of this Chapter as an indication that the common murre

integrates information about its prey field on such scales. This reflects the spatial and temporal scales at which the common murre is likely to find capelin during the breeding season. Regarding the spatial scale, investigations on the capelin spawning dynamics indicate that they undertake extensive migrations from offshore feeding grounds near the edge of the continental shelf (Carscadden *et al.* 1997), as they move closer to the coast they pause in staging areas where they complete gonadal development (Davoren *et al.* 2006). Once gonads are fully mature, shoals of males move inshore where they stay waiting for females, who stay further offshore until ready to spawn. After spawning, a large proportion of spent individuals die (Templeman 1948). Those that survive, mainly females (Shackell *et al.* 1994), move back to the staging areas where they resume their diel vertical movement pattern (Davoren *et al.* 2006), before returning back offshore (Templeman 1948). Regarding the temporal scale, capelin spawns in the study area during a 2- to 3-week period (Leggett *et al.* 1984, Nakashima & Wheeler 2002). Thus, during the common murre's breeding season capelin is found across all, or at least a large part of, the avian foraging range. The Random and Inshore foraging scenarios represent this distribution, as opposed to the Foraging in Dense Spots and Foraging in Dense Spots scenarios, which reflect ephemeral concentrations of capelin.

One weakness of this analysis is that by its nature it imposes a gradient in the amount of information used to fit the models considering the different scenarios (Table 4.2). Therefore, there is the possibility that small sample sizes hindered the models' ability to capture patterns in the Dense Spots and Dense Spots Inshore scenarios. Notwithstanding, I believe that the Random and Inshore foraging scenarios are the best representations of

the spatial and temporal scales at which the murre integrates information about its prey field during the breeding season. Thus, I will only consider these two scenarios in the following Chapter, where I present and discuss the fits of the models presented in Chapter 3.

Tables

Table 4.1. p-values of the Lilliefors test for normality, discriminated by prey category. *: significant at the α_c=0.007 level of significance.

Year	*Capelin*	*Other*
1995	0.61	0.54
1996	0.23	0.39
1997	0.01	0.27
1998	0.67	0.81
1999	0.008	0.96
2004	0.0001*	0.17
2005	0.004*	0.75

Table 4.2. Number of IYGPT sets used to estimate prey availability in each spatial scenario

Year	Random	Inshore	Dense Spots	Dense Spots Inshore
1995	26	13	4	4
1996	24	12	6	5
1997	25	13	4	4
1998	24	12	7	4
1999	25	12	5	2
2004	45	19	7	7
2005	49	27	14	6
Average	31.1	15.4	6.7	4.6

Table 4.3. Goodness-of-fit of the models for the four scenarios considered.

Scenario	χ^2		
	Statistical	Ecological	Hybrid
Random	57.9	38.8	28.6
Inshore	39.4	53.2	41.5
Dense Spots	66.5	54.4	37.2
Dense Spots Inshore	60.4	58.7	44.7

Table 4.4. Mean prey availability (#fish km^{-2}), standard deviation (#fish km^{-2}) and coefficient of variation for the Random and inshore foraging scenarios.

	Random foraging			Inshore foraging		
Prey	*Mean*	*SD*	*CV*	*Mean*	*SD*	*CV*
Small capelin	10355	10736	1.04	22395	32995	1.48
Large capelin	4013	5572	1.39	9082	16544	1.82
Other prey	1667	863	0.52	1977	891	0.45

Figures

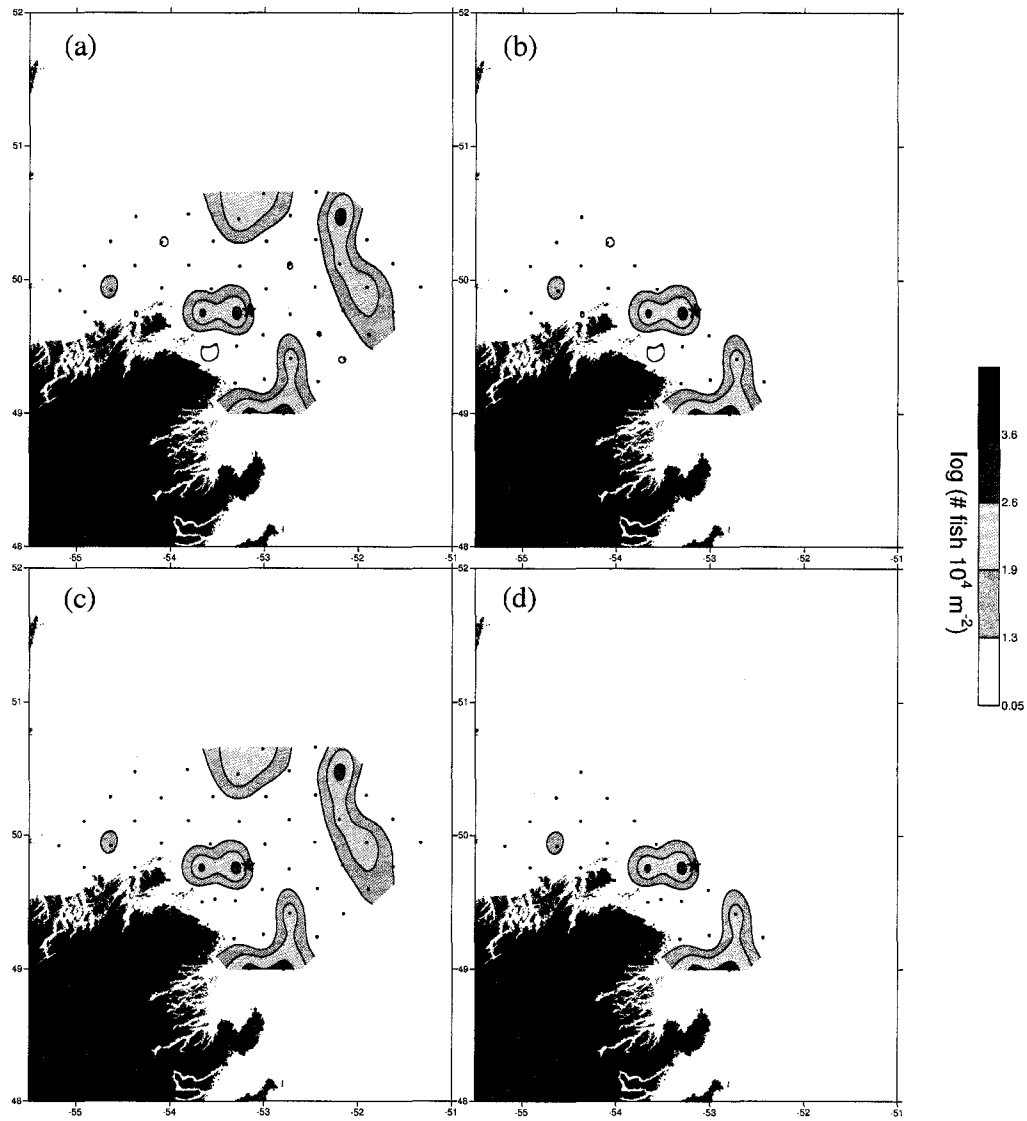


Figure 4.1. Example showing the setting of the spatial scenarios tested. (a) Random foraging, (b) Inshore foraging, (c) Foraging in dense spots, (d) Foraging in dense spots inshore. The dots are trawl locations; the blue star is Funk Island and the shaded areas represent capelin density ($\log_{10}$ number 10^4 m^{-2}). The data correspond to the year 2005.

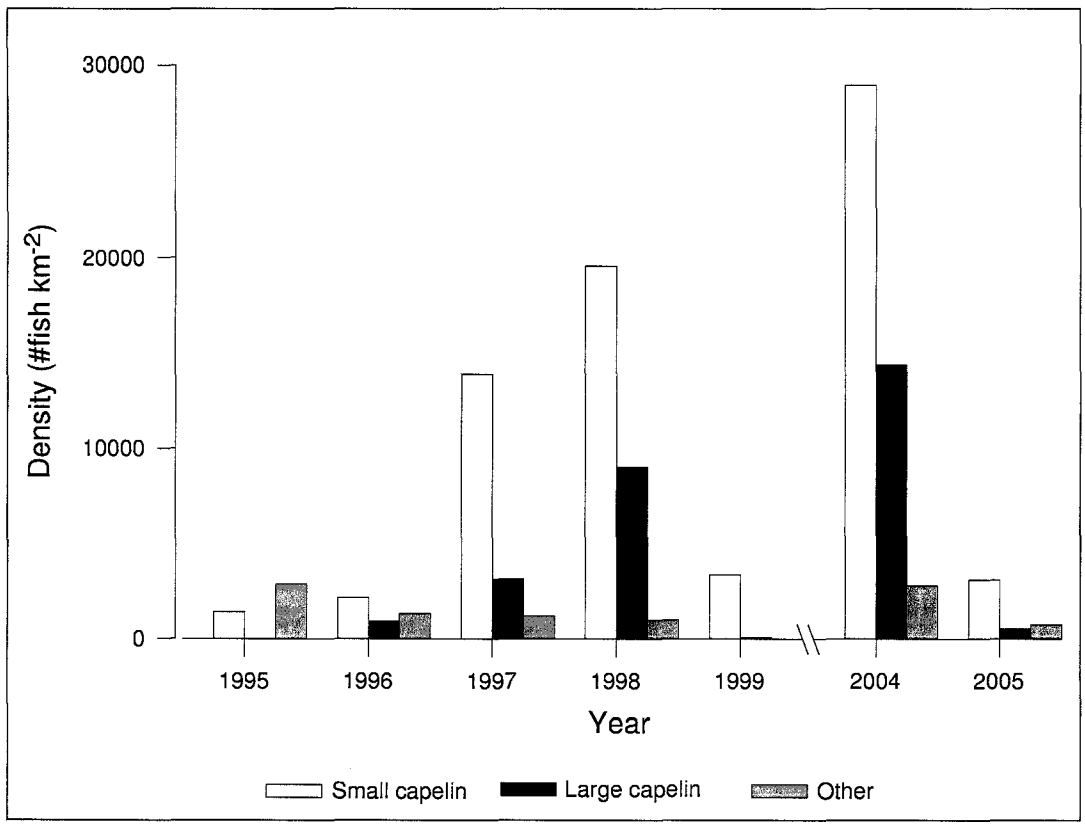


Figure 4.2. Random foraging scenario. Common murre's prey availability around Funk Island, expressed as number of fish per square kilometre. The white bars represent small capelin, the black bars large capelin and the grey bars other prey.

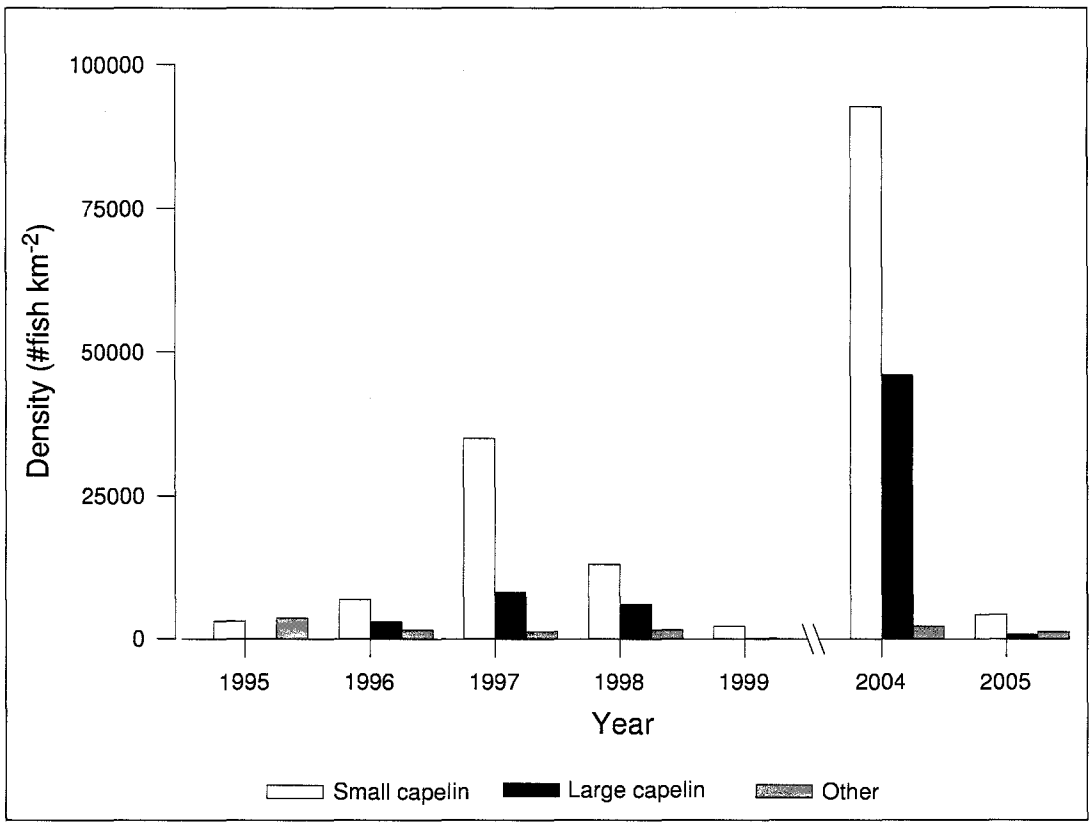


Figure 4.3. Inshore foraging scenario. Common murre's prey availability around Funk Island, expressed as number of fish per square kilometre. The white bars represent small capelin, the black bars large capelin and the grey bars other prey.

Chapter 5

Model fit and selection

Introduction

Predator-prey interactions are arguably the most basic and direct relationships that take place in natural systems. Their outcomes depend largely on the functional form of the prey availability-predator's diet relationship. The form of this relationship entails profound consequences for the predator and prey population dynamics and thus it has been the focus of many articles in the ecological literature; for example recent reviews on predator-prey theory (Murdoch *et al.* 2003, Turchin 2003), and recent reviews and new insights into functional response theory (Jeschke *et al.* 2002, Gentleman *et al.* 2003, Koen-Alonso 2007).

Different functional forms, their outcomes and implications for predator-prey and multi-species models can be explored through the implementation of quantitative models. A fundamental premise of every quantitative ecologist is, in George Box's words; *"all models are wrong, but some are useful"*. All models provide a simplistic and incomplete view of the system's dynamics, and hence when we are faced with the task of understanding how a system works a sound approach to take is to model its dynamics using models that have different structure and thus may provide different insights into the mechanisms that drive them. It is in this spirit that I use three different structural models to gain insights into the link between prey availability and diet. Naturally, they will have different degrees of empirical support and thus they are ranked and the insights gained

from them weighed according to the support they have in the data.

Methods

In this Chapter I describe the fits of the models described in Chapter 3 and rank them following the information-theoretic approach. The prey fields used in this exercise were selected and described in the previous Chapter. Following the model comparison and selection, I interpret the model parameters of the subset of models that show the best fit to the diet data.

Model comparison and selection

An information-theoretic approach was taken in order to rank and select the best model from the suite of competing models described in Chapter 3. In particular, the Akaike information criterion corrected for sample size (AICc) (Burnham & Anderson 2002) was used. The expression of the AICc is $AICc = 2\{-\ln[\mathscr{L}(\theta)]\} + 2n_p\left(\frac{N}{N-n_p-1}\right)$, where N is the number of observed parental deliveries and n_p is the number of estimated parameters in the model.

The Akaike information Criterion is an estimate of the expected, relative distance between the fitted model and the unknown true mechanism that actually generated the observed data. Therefore, the model that has the best fit (*i.e.*, the model that has the most support in the data) will have the smallest AICc value. The important feature of the AICc is not its absolute size, but its relative value and in particular the AICc differences

between models ($\Delta AICc_i$). The differences in AICc are computed as $\Delta AICc_i = AICc_i - AICc_{min}$, where $AICc_{min}$ is the best model's AICc value and $AICc_i$ are the competing models' AICc values. Hence, the larger $\Delta AICc_i$ is, the less plausible it is that the fitted model is the best model, given the data. As a general rule, models having $\Delta AICc_i > 10$ have either essentially no empirical support, and may be omitted from further consideration, or at least those models fail to explain some substantial explainable variation in the data (Burnham & Anderson 2002).

Defining functional response type

In particular for the ecological model, it is of interest to test if the rate of successful search (α_i) is a function of prey density (and hence the functional response is Type III; see Chapter 1). In order to do so, I performed likelihood ratio tests (Hilborn & Mangel 1997), testing the null hypotheses H_{o1}: $b_{sc} = 0$; H_{o2}: $b_{lc} = 0$; H_{o3}: $b_{ot} = 0$.

Results

Considering the Inshore foraging scenario, the hybrid model showed the best fit, while the statistical model had a negligible difference in its ΔAICc value and the value of the ΔAICc for the ecological model was equal to 15.5 (Table 5.1), thus leading me to dismiss it.

When the prey field of the Random foraging scenario was used, again the hybrid model showed the best fit while the ecological model had substantial empirical support

(ΔAICc=2.48) in the data, and the statistical model was omitted from further consideration (ΔAICc=15) (Table 5.1).

Next, I describe the model fits for the four combinations of models-scenarios that are worthy of further examination, according to the description given above.

Inshore Foraging Scenario

Statistical Model

The statistical model (Inshore foraging scenario) fit the observed diet reasonably well (Figure 5.1). The number of large capelin delivered to the chicks was well represented during the years 1997, 2004 and 2005, while during the years 1995 and 1999 it was represented moderately well, with the predictions falling inside (1995) or slightly outside the observations' confidence intervals (1999). The consumption of large capelin during the years 1996 and 1998 was poorly represented, with the residuals (residuals = %N observed - %N predicted by model) being larger than 14 %N. The statistical model estimated the number of small capelin delivered quite accurately for all years, with the exception of 1996 and 1998, when the magnitude of the residuals was 16 %N. The number of other prey delivered was well estimated in all years, except in the years 1998 and 1999 when the residuals had the same order of magnitude as the observed diet.

Hybrid Model

The fit of the hybrid model in the Inshore foraging scenario was almost identical to that

of the statistical model, showing only a slight improvement in the fits of small and large capelin during the years 1996 and 1999 (Figure 5.2).

Random Foraging Scenario

Ecological Model

The behavior of the ecological model (Random foraging scenario) was altogether very satisfactory. It captured most of the characteristics of the time series, some years showing high and others low contrast between the number of small and large capelin delivered to the chicks (Figure 5.3). The number of capelin consumed was very well estimated throughout the study period with the only exception of the year 1999. In particular, it showed a very good fit to the large capelin data for the years 1995, 1997, 2004 and 2005, a somewhat poorer fit to the 1996 and 1998 data, and a rather poor fit to the 1999 data. The estimates of the number of small capelin consumed were accurate for all years, with the highest residuals being smaller than 10 %N (in 1999). The only component of the diet that the ecological model had some difficulty capturing was other prey; during 1996, 1999 and 2004 the residuals had the same order of magnitude as the observed diet.

Hybrid Model

The fit of the hybrid model in the Random foraging scenario was quite similar to that of the ecological model (Figure 5.4), with the only difference that it showed a little improvement in the fits for almost all years, in particular in the year 1996 when the residuals were smaller than 5 %N.

The rather poor performance of all models to explain the diet composition of the years 1996, 1998 and 1999 does not seem to be due to inability of the models to explain the variability in the diet; it is because of the sample sizes not being large enough (Table 2.2). In all cases, there is a considerable reduction in the residuals with increasing sample size (Figure 5.5), and when the sample size is larger than 100 they stay fairly constant at values equal to or smaller than 6 %N. This pattern in the residuals was observed because an unweighted fit was performed, therefore each datum (parental delivery) was given equal weight when calculating the model's likelihood. It follows that the models show an increasingly better fit with sample size.

Model selection

Although the Akaike Information Criterion can not be used to compare the fit of the models between scenarios, visual inspection leads me to draw my attention exclusively to the models fit using the prey availabilities estimated in the Random foraging scenario because they describe the patterns in the data more parsimoniously. Specifically, the models fitted considering the Inshore foraging scenario (Figures 5.1 and 5.2) failed to capture the high contrast shown in the consumption of small and large capelin in 1996 (with the predictions falling well outside the confidence intervals), while the models fitted considering the Random foraging scenario did capture it, and their predictions fell inside the confidence intervals (Figures 5.3 and 5.4). Furthermore, the predicted consumption pattern of those prey in 1998 is the opposite of the observed pattern in the

diet. On the other hand, although the models fitted considering the Random foraging scenario did not fully capture the observed pattern, their predictions are more accurate; the magnitude of the residuals ranged from 0.06 to 0.1 while the residuals of the models fit considering the Inshore foraging scenario ranged from 0.16 to 0.2.

Thus, I dismiss the models fitted using the prey field considering the Inshore foraging scenario and focus only on the ecological and hybrid models considering the Random foraging scenario.

Parameter interpretation

The values of the maximum likelihood estimates (MLE) of the parameters of the ecological model are presented in Table 5.2. The a_i parameters are just scale parameters and the b_i are the parameters that define the type and shape of the functional response. Thus, I will focus on the latter making only a small comment on the former; note that a_{lc} was not estimated but it was *a priori* set equal to 1 (as large capelin was set as the reference category), thus making the rest of the parameters relative to it. Regarding the b_i parameters, the shape parameters, their MLEs are all different from zero and took negative values (Table 5.2). In general terms, the ranges of values of the b_i parameters that fell within their respective 95% CI were quite narrow with respect to their MLEs (only 1 order of magnitude bigger), while the range for the a_i parameters were much wider (2 and 3 orders of magnitude bigger than their MLEs for a_{sc} and a_{ot} respectively; Figure 5.6). In particular for the b_i parameters, it is interesting to note that the range for b_{lc} was the narrowest among the three, while the one for b_{ot} was the widest. This responds

to the amount of information for each prey category in the diet data; the prey for which there is more data has the smallest CI and the one with the least information (Table A.1) has the biggest CI (relative to their MLEs).

The likelihood ratio tests performed for defining the type of functional response exhibited by the common murre showed that the parameters b_{sc} and b_{lc} are significantly different from zero while b_{ot} is not (Table 5.3). Therefore, a_{sc} and a_{lc} are functions of prey density and hence the common murre's multi-species functional response is of Type III (see Chapter 1).

This functional response is a multi-dimensional function and thus can not be represented graphically. In order to visualize the functional response curve, and for ease of interpretation, I plotted the three single-species functional response curves, each one corresponding to a prey category (Figures 5.7, 5.8 and 5.9). These plots were obtained by keeping the values of prey availability of two prey fixed at their average values while for the third prey (the one shown in the corresponding figure as explanatory variable) the values were varied in equal increments, covering the range of prey availabilities observed. However, one must bear in mind that there is an underlying multi-species functional response to the three single-species ones. I also plotted the surfaces that represent the functional responses with respect to small and large capelin, both shown as a function of these two prey availabilities (Figures 5.10 and 5.11). The three single-species curves have a hyperbolic shape, this results from the exponents (λ_i) taking values between zero and one (Table 5.2), which means that the single-species functional responses increase as the *k*th root of prey density. However, they increase at different

rates; FR_{ot} increases almost linearly (*i.e.*, $b_{ot} + 1 \cong 1$), while FR_{sc} increases somewhat slower and FR_{lc} presents the slowest rate of increase (Table 5.2). The surfaces that represent the murre's functional response with respect to small and large capelin exhibit the same pattern; the functional response with respect to small capelin (Figure 5.10) is a monotonic increasing function of the density of that prey and an inverse function of the density of large capelin, and conversely for the functional response with respect to large capelin (Figure 5.11) .

One last point that is worth mentioning regarding the MLE of the shape parameters is that all took negative values, *i.e.* the rate of successful search (α_i) is inversely dependent on the density of the *i*th prey (Figures 5.12, 5.13 and 5.14). This means that although the capture rate of the *i*th prey (C_i) increases with prey density (Figures 5.15, 5.16 and 5.17), the prey consumption rate per-capita of prey decreases.

Regarding the parameters of the hybrid model, their interpretation is not as simple as the ecological model's parameters. In order to properly interpret them one must be aware of the category that was chosen as baseline; in this Thesis I chose large capelin as the baseline category for all the models used (Chapter 3). The intercept parameters (B_i) are not of interest, we are interested in the parameters that indicate the effect that prey density has on the probability of consuming a given prey ($\gamma_{m,i}$). The simplest interpretation is as follows: $e^{\gamma_{m,i}}$ is an odds ratio, the odds that the common murre chooses prey *i* instead of large capelin (reference category) at prey density $\ln(N_m)$ divided by the odds of choosing prey *i* instead of large capelin at prey density $\ln(N_m + 1)$. In other words, it is a measure of the effect that a 1-unit increase in the log density of prey *m* has

on the odds of choosing prey *i* instead of the prey chosen as baseline (it measures the effect of a 1-unit increase in the log density of prey because in the hybrid model the probability of consuming the *i*th prey is a function of prey densities in a logarithmic scale). Since many people are not familiar with odds ratios, I give a brief description of their interpretation. If an odds ratio is equal to 1 then a change in the density of prey *m* has no effect on the odds of choosing prey *i* instead of large capelin, if it is larger than 1, then an increase in the density of prey *m* increases the odds of choosing prey *i* instead of large capelin and it decreases the odds if the odds ratio is smaller than 1. The MLE of the odds ratios, along with their 95% confidence intervals, are presented in Table 5.4. A 1-unit increase in the log density of small capelin significantly increases the odds that the common murre chooses small capelin ($\gamma_{sc,sc}$) and other prey ($\gamma_{sc,ot}$) instead of large capelin. On the contrary, an increase in the log density of large capelin significantly decreases the odds that the common murre chooses small capelin ($\gamma_{lc,sc}$) or other prey ($\gamma_{lc,ot}$) instead of large capelin. Finally, an increase in the log density of other prey has no significant effect on the odds of choosing either small capelin ($\gamma_{ot,sc}$) or other prey ($\gamma_{ot,ot}$) instead of large capelin.

Discussion

I ranked and selected the best models from the suite of competing models described in Chapter 3, considering the scenarios chosen as being the best descriptions of the prey field in Chapter 4. Next, I described the model fits and based on that description I focused my attention exclusively on the ecological and hybrid models, considering the Random

foraging scenario. At last, I presented the MLE of the models parameters and described their interpretation.

Overall, the four models described in this Chapter captured reasonably well the main features of the common murre's diet. The biggest discrepancies between observed and expected values were a result of small sample sizes, not of model inadequacy.

However, a much better fit was achieved when the prey density estimates were done according to the Random foraging scenario. Following on the same rationale as in the previous Chapter, I think that the Random foraging scenario provides the best description of the prey field since it reflects the spatial scale at which the common murre integrates information. The most likely cause for outperforming the Inshore foraging scenario is that the area not considered in the latter scenario is not only a potential feeding ground, but some flocks of common murres have actually been seen foraging there (C. Burke, *pers. comm.*).

The two best models (ecological and hybrid) in this scenario showed a very satisfactory fit to the diet data, and although the hybrid model showed a slightly better fit I allege that the ecological model is preferred over it because of two reasons. In the first place, its derivation is based on ecological concepts and hence it can be readily interpreted in terms of the processes that determine the predator-prey interactions. On the other hand, the interpretation of the parameters of the hybrid model is counterintuitive and somewhat awkward. Therefore, given that the improvement in fit of the hybrid over the ecological model is only very slight, that the ecological model can be interpreted in ecological terms and that the parameters of the hybrid model are not easily interpretable I conclude that

the ecological model, when using the prey abundance estimates derived from the Random foraging scenario, is the best choice among the suite of competing models described in this Thesis.

Nevertheless, fitting the hybrid model provided an interesting insight into how the murre perceives its prey field. Only a change in the density of either small or large capelin has a significant effect on the odds of choosing a given prey category, changes in other prey density have no significant effect on the probability of consuming any of the prey categories. Furthermore, changes in the densities of small and large capelin exert the same effect on the probability of consuming small capelin and other prey, *i.e.* when large capelin density increases, the probability of consuming small capelin and other prey decreases and the probability of consuming large capelin increases, while an increase in small capelin density has the opposite effect on the probabilities of consuming the different prey categories. I interpret this as a reflection of the murre's perception of its prey field; I hypothesize that the common murre only perceives capelin as prey, distinguishing between small and large and mistaking other prey for small capelin. In order to test this hypothesis, a prey preference analysis should be conducted (Chesson 1978). This analysis should consider prey availabilities discriminated by size as well as diet. Unfortunately, the length frequency distribution of other prey is not available, and thus the analysis can not be carried out. However, the hypothesis finds circumstantial support in the fact that 85% (55 out of 65) of the fish considered as other prey that were measured were smaller than 140 mm. This would render recognizing other prey from small capelin while in flight very difficult. Most likely, all the other prey taken were

juvenile pelagic stages and, therefore, the common murre mistook aggregations of these juveniles for aggregations of capelin.

In order to discuss the results of the ecological model I introduce a fundamental concept for the classification of functional responses: prey switching. Murdoch (1969) defined that switching in predators occurs when the number of attacks upon a species is disproportionately large when the species is abundant relative to other prey, and disproportionately small when the species is relatively rare. Following Koen-Alonso's (2007) criterion for classifying multi-species functional responses, I classified the common murre's functional response as Type III. An alternative MSFRs classification was proposed by Gentleman *et al.* (2003), they classify MSFRs into 3 categories according to their potential to produce prey switching: Class 1, Class 2 and Class3. The Class 1 MSFR doesn't produce prey switching, Class 2 produces passive switching (*i.e.* it arises from factors causing different SSFR and hence can be predicted from them) and Class 3 produces active switching (*i.e.* the switching is due to behaviors that depend on the relative densities of two resources in a manner that may not be predicted from the SSFR). In this framework, the MSFR equation (Eq. 11) used in this Thesis is a Class 2 functional response. This is a direct result of the rate of successful search (α_i) being a function of the *i*th prey density. It is then interesting to note that Koen-Alonso's (2007) rationale for classifying prey-dependent MSFR as Type III is shared with Gentleman *et al.*'s (2003): it's based on the potentiality to produce prey switching.

A point worth of attention is the fact that the b_i parameters of the common murre's functional response took negative values (Table 5.2), a situation not considered by Koen-Alonso (2007). This author defines the parameter b_i as a positive constant coefficient (p. 15 in Koen-Alonso 2007). When developing his classifying criteria, Koen-Alonso (*pers. comm.*) tried to define MSFRs that if collapsed to SSFRs would agree with the traditional functional response classification, and thus defined b_i in such a way that it would produce a sigmoidal SSFR. However, there is no logical reason why the values that this parameter can take should be restricted to be larger than one. Actually, the functional response is defined for the range of b_i $(-\infty, \infty)$ and it can be interpreted in ecological terms, depending on the parameter's value:

i. if $b_i = 0$, then the rate of successful search is independent of prey density, therefore this functional response can not produce prey switching. Hence, it can be typified as Class 1 in Gentleman *et al.*'s (2003) framework or Type II in Koen-Alonso's (2007).

ii. if b_i is in the range $(-1, 0 \cup 0, \infty)$, this functional response can produce prey switching and is a monotonic increasing function of prey density. Therefore, it may be classified as Class 2 following Gentleman *et al.* (2003) or as Type III following Koen-Alonso (2007) (provided that we relax Koen-Alonso's definition to include negative values of b_i)

iii. if $b_i = -1$, then the functional response is a constant. It is hard to imagine a predator that would consume prey at a constant rate, although one may imagine this function as an approximation of the functional response of a predator that

reaches its saturation point very easily. This functional response would be classified as Class 1 following Gentleman *et al.* (2003), while it can not be classified following Koen-Alonso (2007).

iv. if b_i is in the range ($-\infty$, -1), the functional response can produce prey switching and it decreases with prey density. Thus, it can be classified as Class 2 in Gentleman *et al.*'s (2003) framework or as Type IV in Koen-Alonso's (2007). The key element to distinguish a Type III from a Type IV functional response is that in the former as prey density tends to infinity, consumption tends to infinity while in the latter as prey density tends to infinity, consumption tends to zero.

The common murre's functional response falls in the second case: the values of the b_i parameters are in the range (-1, 0), and therefore the exponents (λ_i) are in the range (0, 1). This situation was previously described by Real (1977). This author interprets the exponent (λ_i)[§] in the expression of the functional response (Eq. 5) as the number of encounters a predator must have with a prey item before becoming maximally efficient at utilizing it as a resource. Real (1977) explicitly considered the case when the exponent is in the range (0, 1) in his interpretation of Type III functional responses and noted that the rate of successful search would decrease with increasing prey density.

It is interesting to note that had I followed the traditional single-species classification, I would have concluded the functional responses with respect to the three prey to be Type

[§] Real (1977) used '*n*' to denote the exponent in the expression of the functional response

II. This stresses the fact that classifying a multi-species functional response based on graphical criteria may be misleading, exalts the need of adopting explicit mathematical criteria for the classification of functional responses and underlines the importance of evaluating the parameters of the functional response (most importantly the shape parameters b_i).

An interesting insight gained from the ecological model is that the common murre's prey consumption increases with prey density, while the rate of successful search decreases. Three plausible, non-mutually exclusive explanations may be given for this fact:

i. Capelin's predator avoidance mechanisms improve as group size increases.

Shoaling fish may counter predator attack through a variety of mechanisms, such as predator avoidance, detection, evasion, inspection and confusion, risk dilution, attack inhibition and mitigation (reviewed in Pitcher & Parrish 1993). Most of these mechanisms are more efficient when fish group in larger shoals.

ii. Dense aggregations of prey may attract seabirds thus promoting interspecific competition for resources.

Common murres cue on the activities of conspecifics to reduce search costs for capelin. However, prey consumption rates may be diminished by competitive interactions during prey capture at high seabird densities (Davoren *et al.* 2003c).

iii. The common murre exhibits negative prey switching.

Negative prey switching would imply that the common murre consumes disproportionately less of a given prey category when the species is abundant

relative to other prey, and disproportionately more when the species is relatively rare.

I argue that the common murre exhibits negative prey switching based on two premises. First, central place foraging theory (Orians & Pearson 1979) predicts that as distance, and hence traveling time, from the foraging patch to the central place increases, the greater must be the prey energy selected by the predator. Burke (*in prep.*) found that parental common murres breeding on Funk Island conform to this prediction, since in 2005 (low capelin availability) they flew farther and delivered more profitable prey (large capelin) than in 2004 (high capelin availability). On the other hand, relative large capelin density (with respect to small capelin density) increases with 'suitable' capelin density (Figure 5.18). Therefore, in years of low capelin availability, large capelin is relatively rare (with respect to small capelin), and the common murre consumes disproportionately more of it and vice versa, thereby complying with the definition of negative prey switching. How does negative prey switching relates to the rate of successful search? The rate of successful search is defined as $\alpha_i = a_i N_i^{b_i}$. In order for prey switching to occur the 'pairwise relative preference' (φ_{ij}: the predator's preference of prey *i* with respect to prey *j*) must be variable (Koen-Alonso 2007). For the generalized Holling multi-species functional response, $\varphi_{ij} = \frac{a_i N_i^{b_i}}{a_j N_j^{b_j}}$ (Koen-Alonso 2007). Therefore, in order for negative prey switching to occur the exponent b_i must be negative; in that way

the preference for prey *i* decreases as its density increases. This implies that if the predator exhibits negative prey switching the rate of successful search is a decreasing function of prey density.

In the light of this argument, I hypothesize that if the most profitable prey item of a central place forager becomes proportionally less available as total prey availability decreases, then the central place forager will exhibit negative prey switching (and consequently its rate of successful search will be a decreasing function of prey density).

While I dealt with structural uncertainty by fitting models with different structure and ranking their performance, I have not addressed parameter uncertainty in this Thesis. The parameters of the function relating prey availability to the common murre's diet were estimated from field data, which are subject to process and observation error. Therefore, there must be inherent uncertainty in the values of the parameter estimates. An analysis of parameter uncertainty should be a focus of further development in the common murre-capelin interaction. The use of Bayesian statistics (Gelman *et al.* 2004) represents a promising approach in this respect (see Harwood & Stokes 2003).

Tables

Table 5.1. Comparison of the best fits among the statistical, ecological and hybrid models, considering the Inshore and Random foraging scenario. n_p: number of estimated parameters.

	Statistical	Ecological	Hybrid
n_p	8	5	8
	(A) Inshore foraging scenario		
ΔAICc	0.80	15.55	0
	(B) Random foraging scenario		
ΔAICc	15.00	2.48	0

Table 5.2. Maximum likelihood estimates of the parameters and values of the exponent (λ_i) of the ecological model, considering the Random foraging scenario.

Parameter	*MLE*
a_{sc}	0.009
a_{lc}	1
a_{ot}	0.0007
b_{sc}	-0.25
b_{lc}	-0.70
b_{ot}	-0.04
λ_{sc}	0.75
λ_{lc}	0.30
λ_{ot}	0.96

Table 5.3. Likelihood ratio tests for defining functional response type. *: significant at the 0.05 level of significance.

Hypothesis	$\ln[\mathscr{L}(\theta)]$	$\mathscr{R}$	*d.f.*	*p-value*
$b_i \neq 0$	-794.688			
$b_{sc} = 0$	-797.172	4.97	1	0.025*
$b_{lc} = 0$	-872.461	155.55	1	<0.00001*
$b_{ot} = 0$	-794.695	0.01	1	0.91

Table 5.4. Odds ratio estimates (with their 95% confidence intervals) of the hybrid model, considering the Random foraging scenario. Note that the parameter to which the odds ratio corresponds is between brackets, $e^{\gamma_{m,i}} = \pi_i / \pi_{lc}$

Explanatory variable (N_m)	*Odds Ratio*	*Point estimate*	*95% Wald Confidence limits*
Density Small Capelin	$\pi_{sc}/\ \pi_{lc}$ $[\gamma_{sc,sc}]$	2.7	1.8 - 4
Density Small Capelin	$\pi_{ot}/\ \pi_{lc}$ $[\gamma_{sc,ot}]$	4.5	1.2 - 16.8
Density Large Capelin	$\pi_{sc}/\ \pi_{lc}$ $[\gamma_{lc,sc}]$	0.7	0.6 - 0.8
Density Large Capelin	$\pi_{ot}/\ \pi_{lc}$ $[\gamma_{lc,ot}]$	0.4	0.2 - 0.7
Density Other Prey	$\pi_{sc}/\ \pi_{lc}$ $[\gamma_{ot,sc}]$	0.9	0.6 - 1.2
Density Other Prey	$\pi_{ot}/\ \pi_{lc}$ $[\gamma_{ot,ot}]$	1.3	0.5 - 3.4

Figures

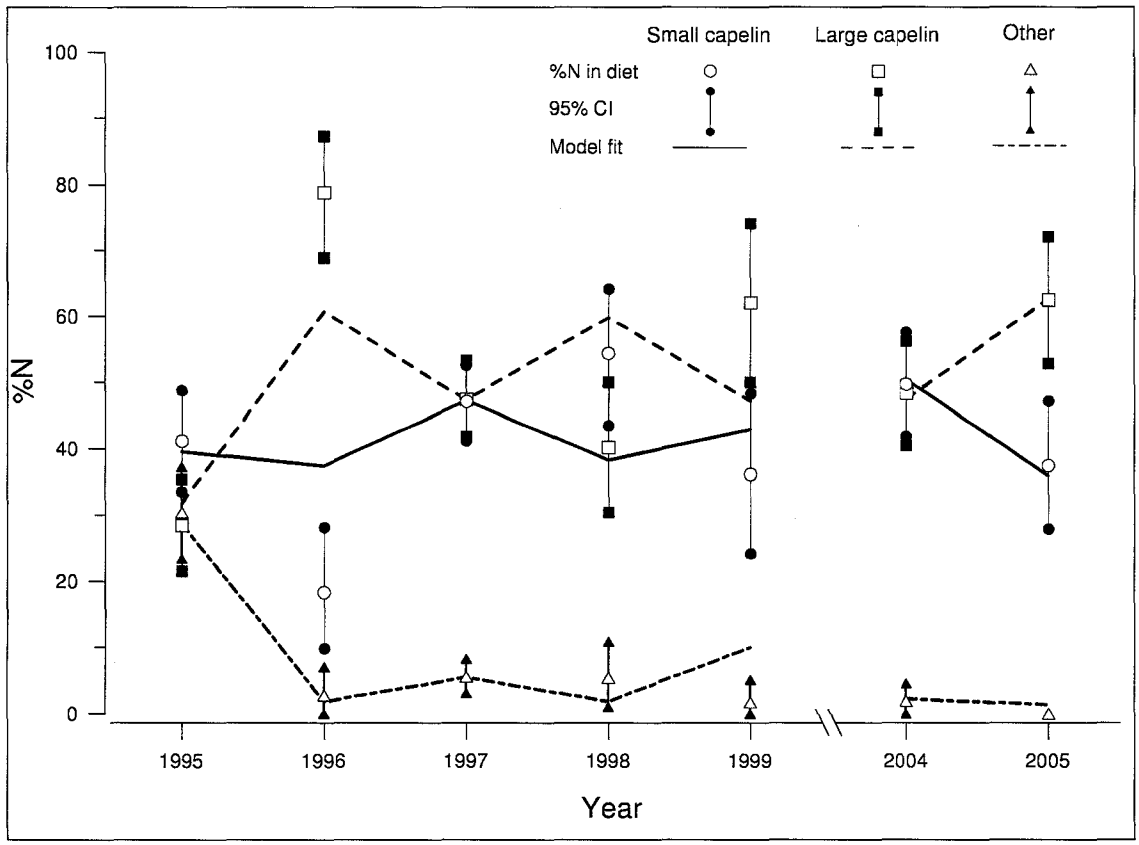


Figure 5.1. Fit of the statistical model to the diet data, considering the Inshore foraging scenario. The circles, squares and triangles are point estimates of the %N that small capelin (100-140 mm), large capelin (>140 mm) and other prey represent in the common murre's diet, respectively. The bars indicate bootstrap 95% CI and the lines represent the model fit.

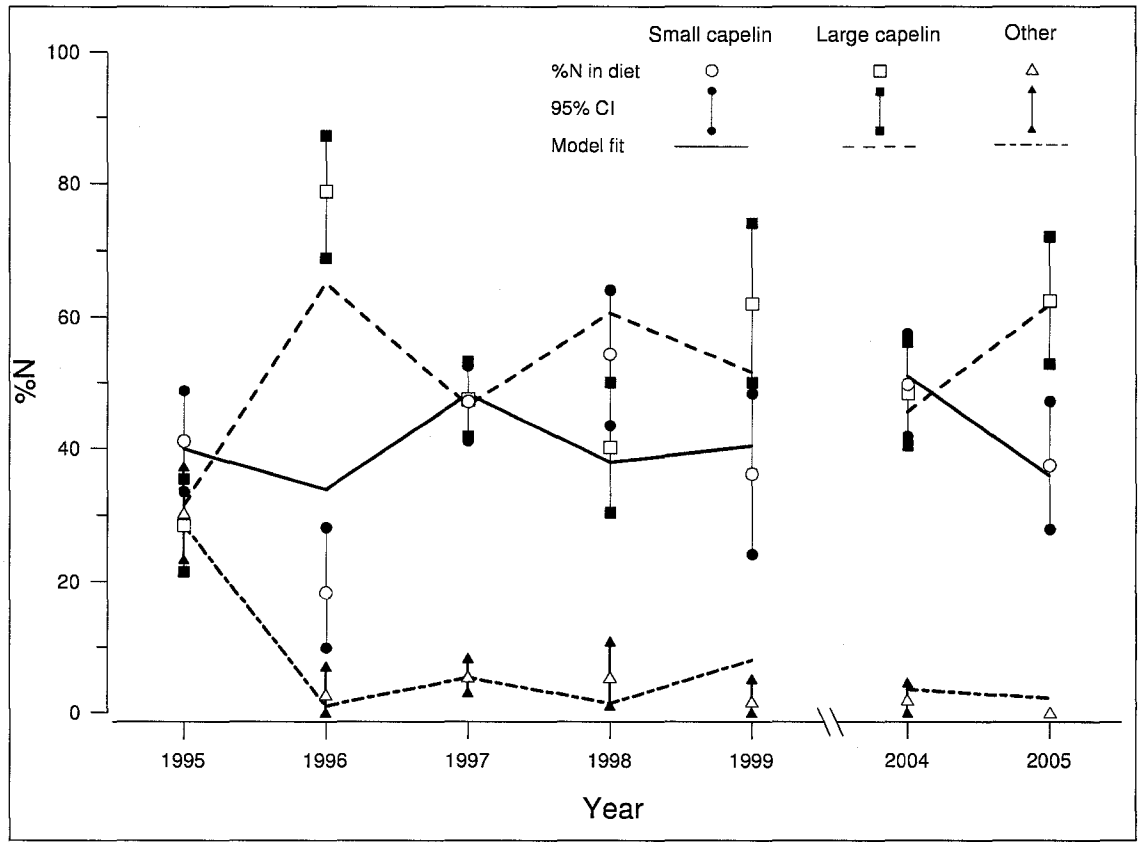


Figure 5.2. Fit of the hybrid model to the diet data, considering the Inshore foraging scenario. The circles, squares and triangles are point estimates of the %N that small capelin (100-140 mm), large capelin (>140 mm) and other prey represent in the common murre's diet, respectively. The bars indicate bootstrap 95% CI and the lines represent the model fit.

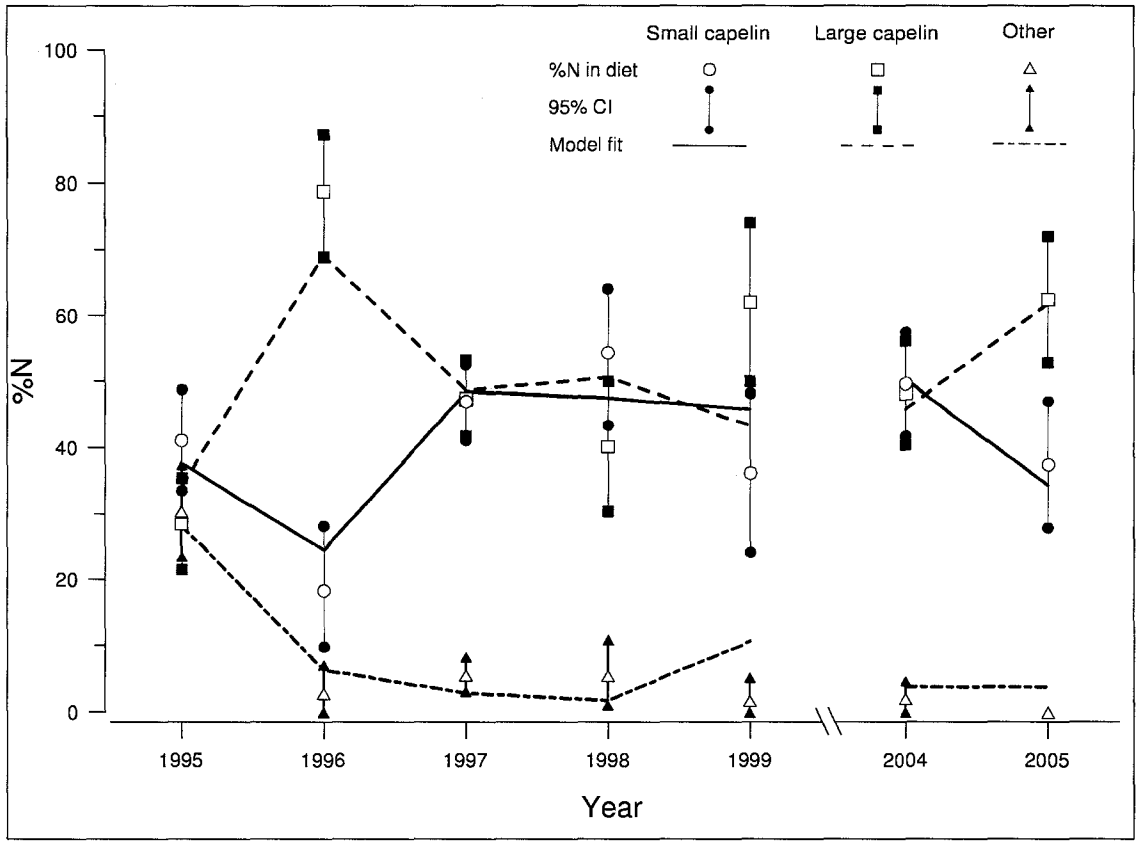


Figure 5.3. Fit of the ecological model to the diet data, considering the Random foraging scenario. The circles, squares and triangles are point estimates of the %N that small capelin (100-140 mm), large capelin (>140 mm) and other prey represent in the common murre's diet, respectively. The bars indicate bootstrap 95% CI and the lines represent the model fit.

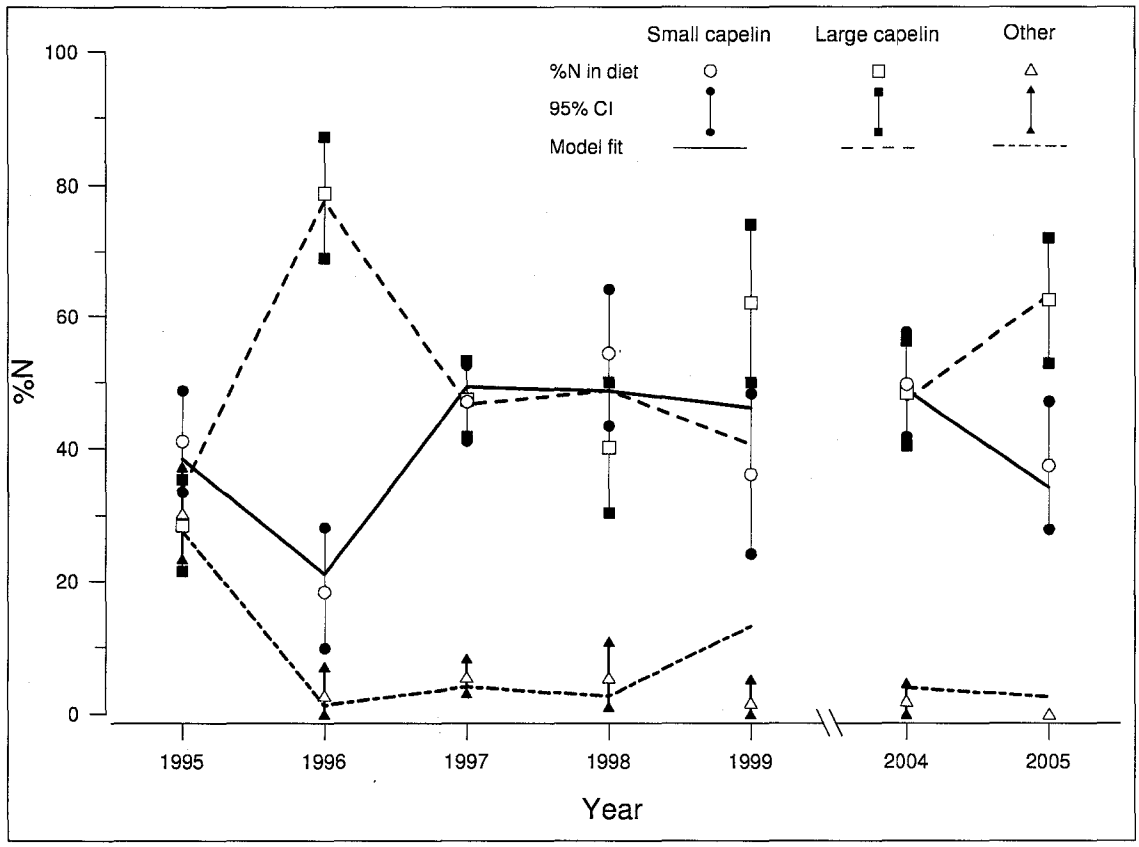


Figure 5.4. Fit of the hybrid model to the diet data, considering the Random foraging scenario. The circles, squares and triangles are point estimates of the %N that small capelin (100-140 mm), large capelin (>140 mm) and other prey represent in the common murre's diet, respectively. The bars indicate bootstrap 95% CI and the lines represent the model fit.

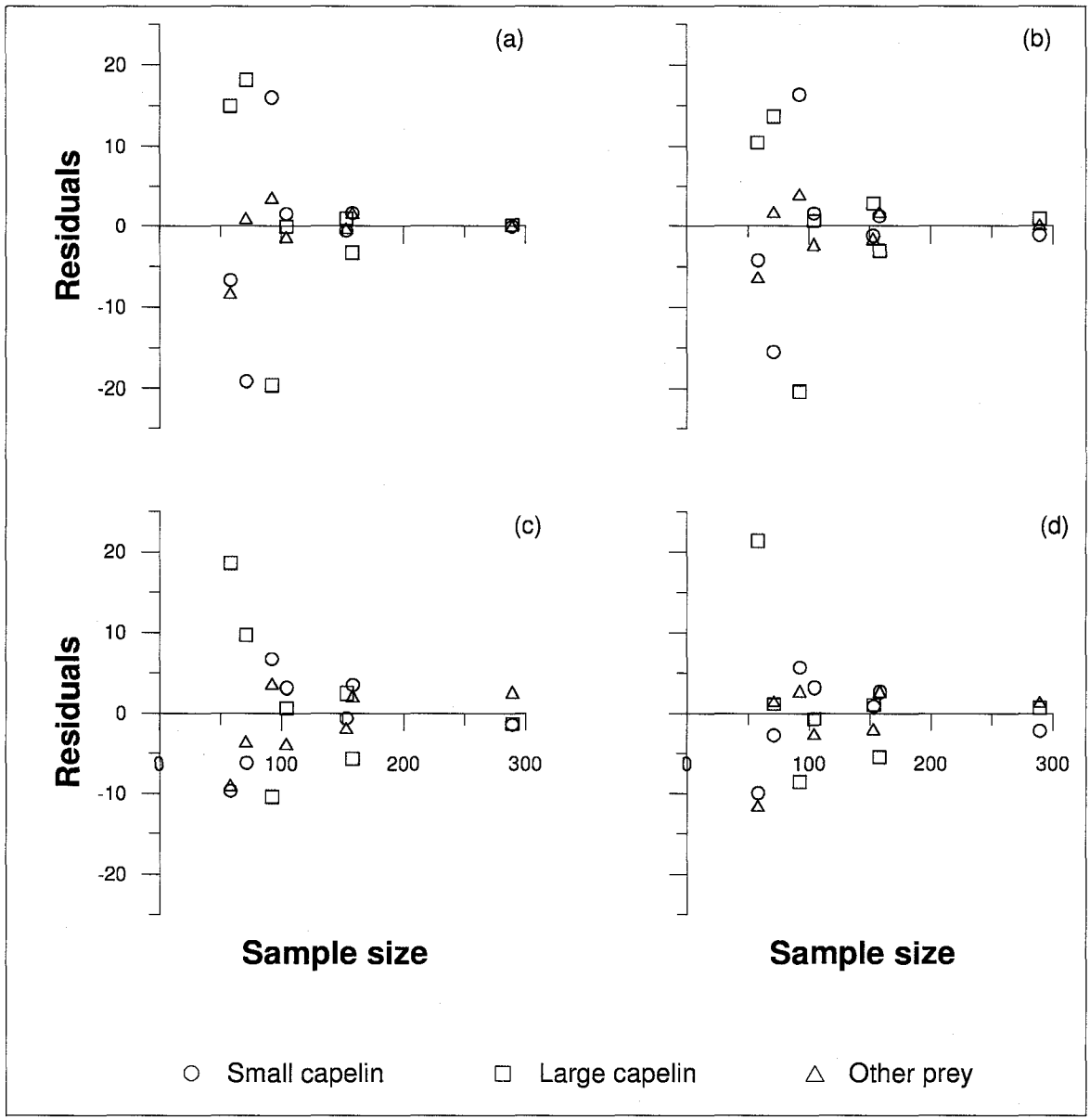


Figure 5.5. Residuals of the models fitted to the diet data. (a) Statistical model, Inshore foraging scenario; (b) hybrid model, Inshore foraging scenario; (c) ecological model, Random foraging scenario; (d) hybrid model, Random foraging scenario.

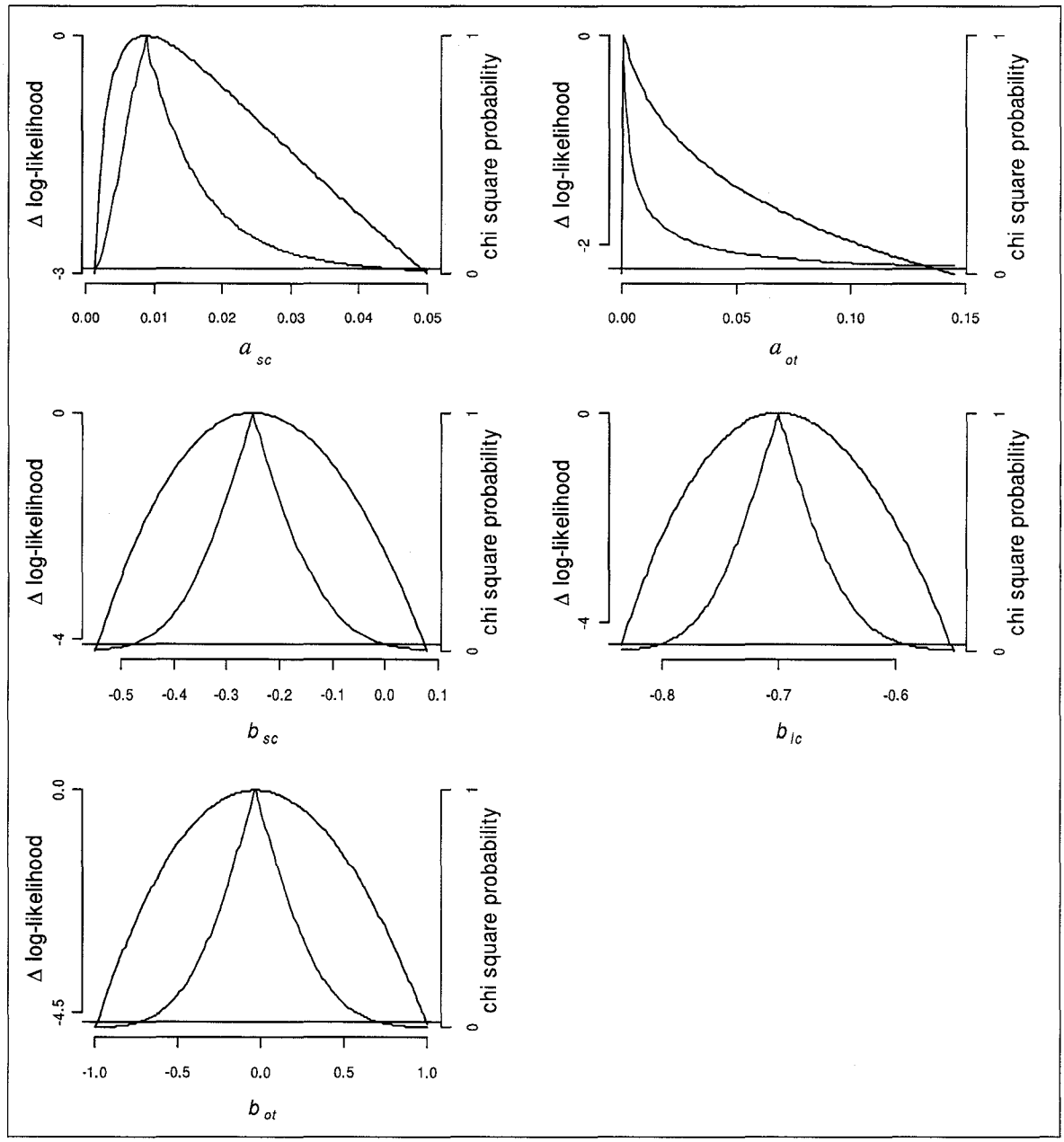


Figure 5.6. Likelihood profiles for the parameters of the ecological model. The blue lines represent the differences in log-likelihoods and the red lines the χ^2 probabilities associated with the LRTs at each value of the parameters. The constant (black line) represents p=0.025.

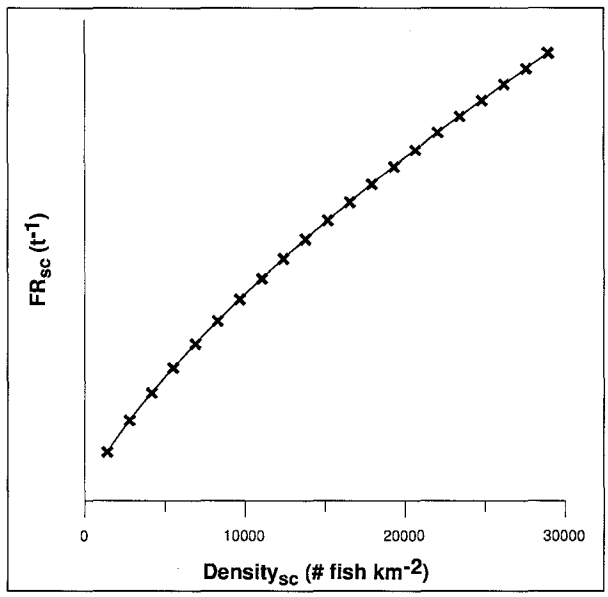


Figure 5.7. Shape of the curve of the common murre's functional response with respect to small capelin, shown as a function of the availability of small capelin.

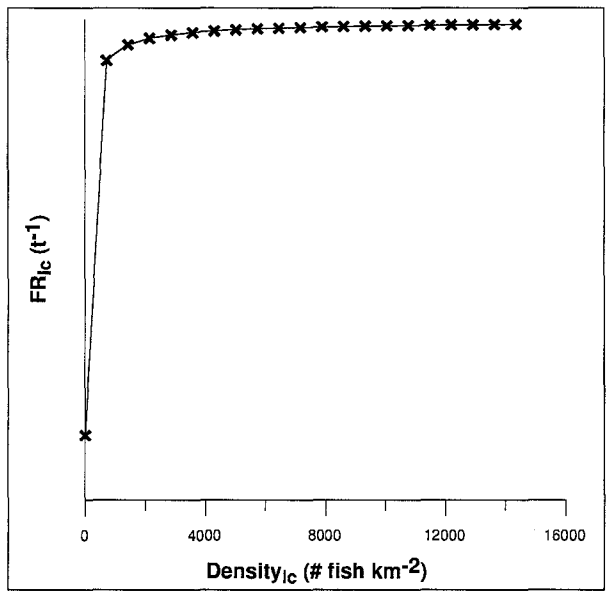


Figure 5.8. Shape of the curve of the common murre's functional response with respect to large capelin, shown as a function of the availability of large capelin.

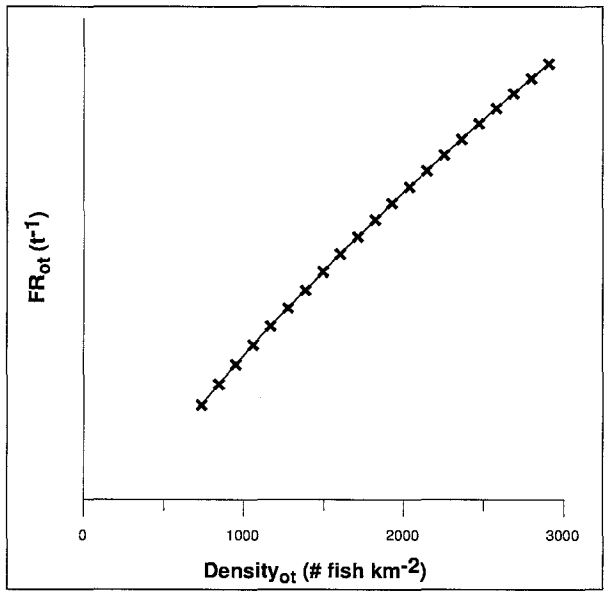


Figure 5.9. Shape of the curve of the common murre's functional response with respect to other prey, shown as a function of the availability of other prey.

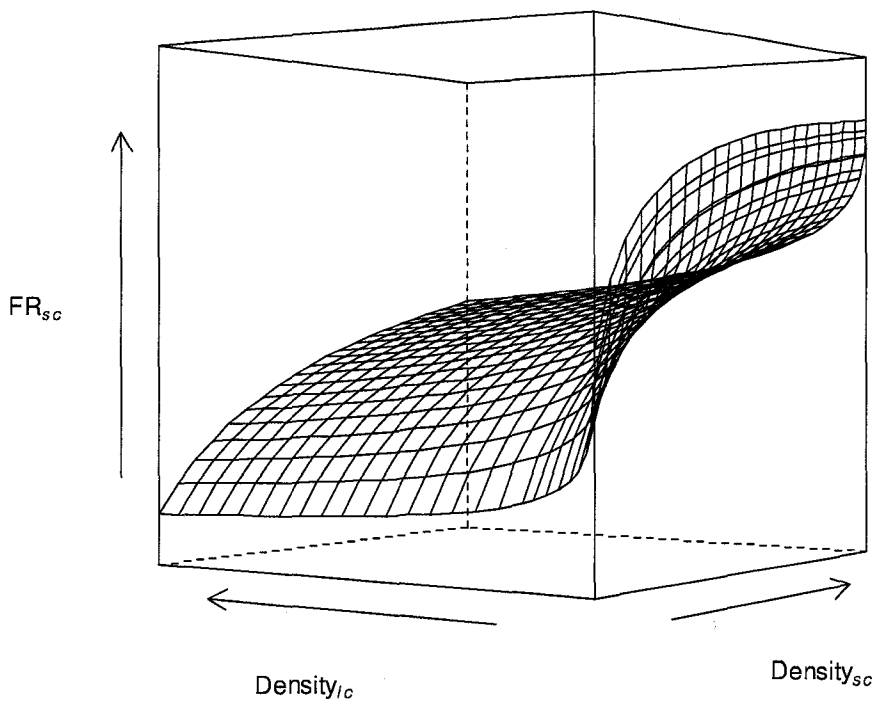


Figure 5.10. Shape of the surface of the common murre's functional response with respect to small capelin, shown as a function of the availability of small and large capelin.

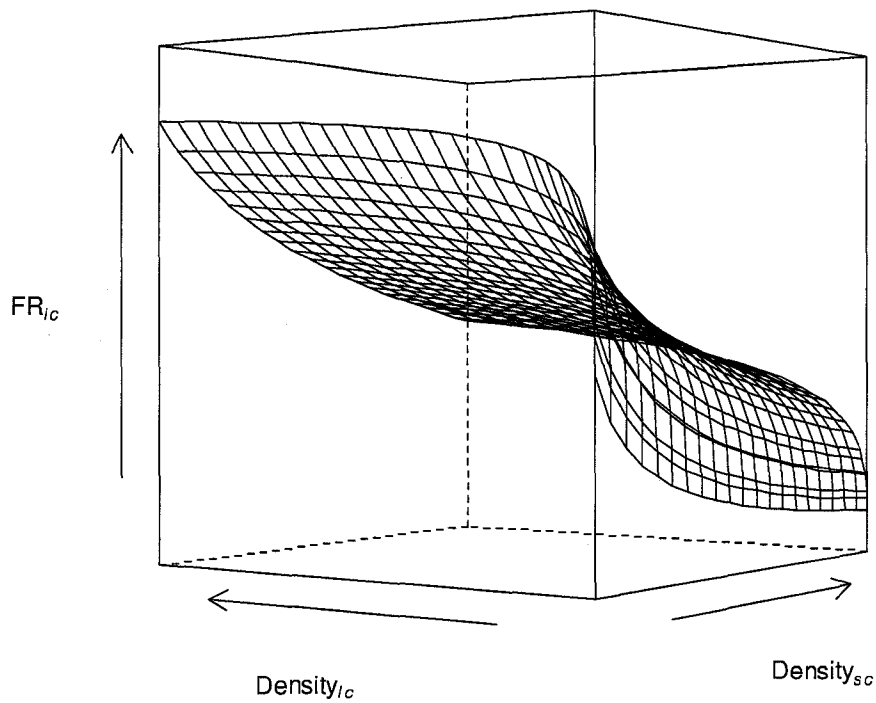


Figure 5.11. Shape of the surface of the common murre's functional response with respect to large capelin, shown as a function of the availability of small and large capelin.

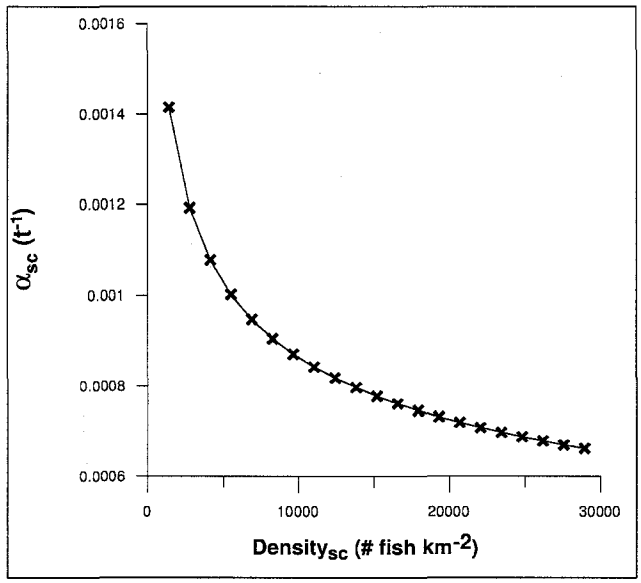


Figure 5.12. 'Rate of successful search' for small capelin, as a function of small capelin density.

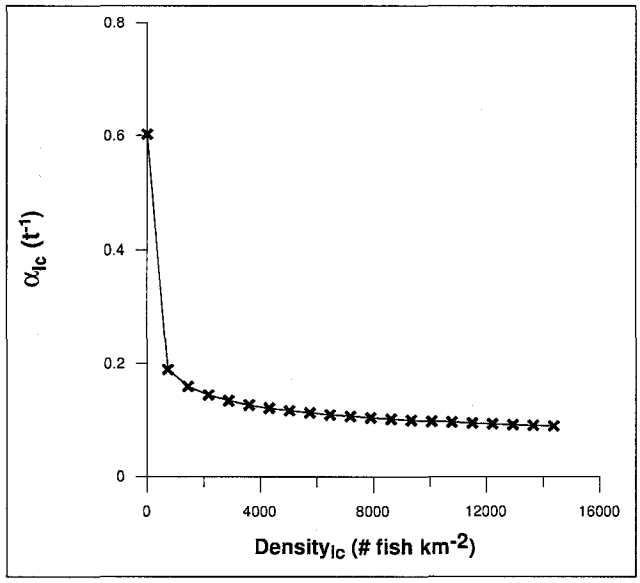


Figure 5.13. 'Rate of successful search' for large capelin, as a function of large capelin density.

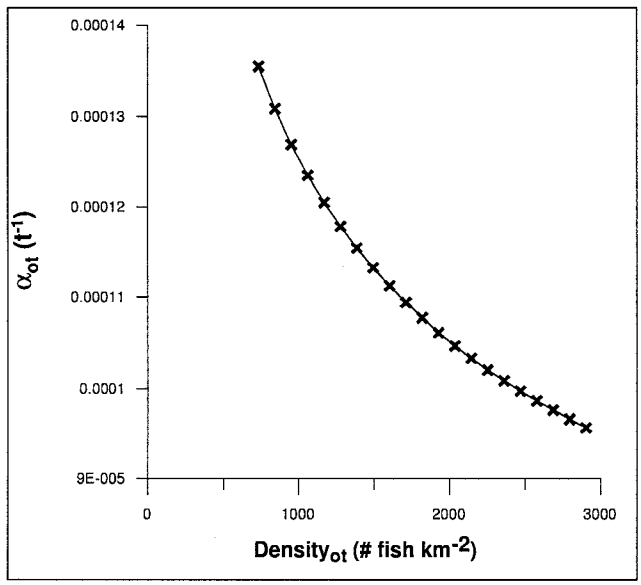


Figure 5.14. 'Rate of successful search' for other prey, as a function of other prey density.

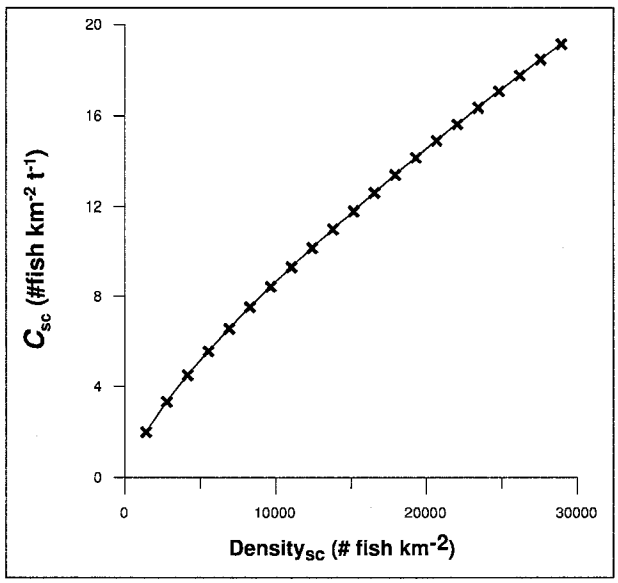


Figure 5.15. Capture rate of small capelin, as a function of small capelin density.

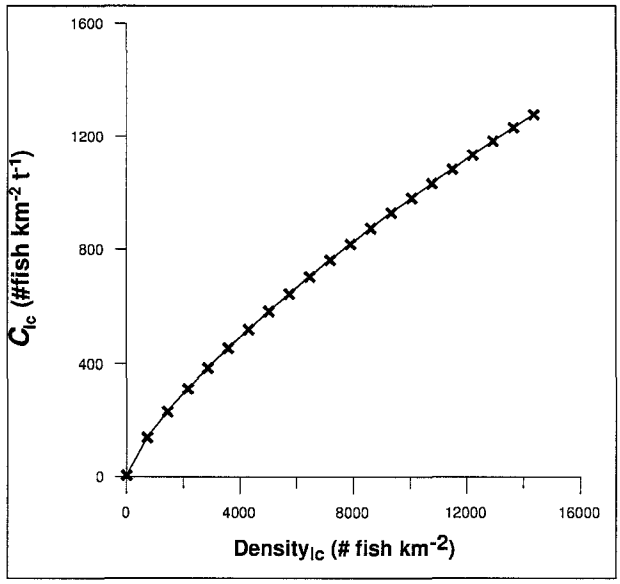


Figure 5.16. Capture rate of large capelin, as a function of large capelin density.

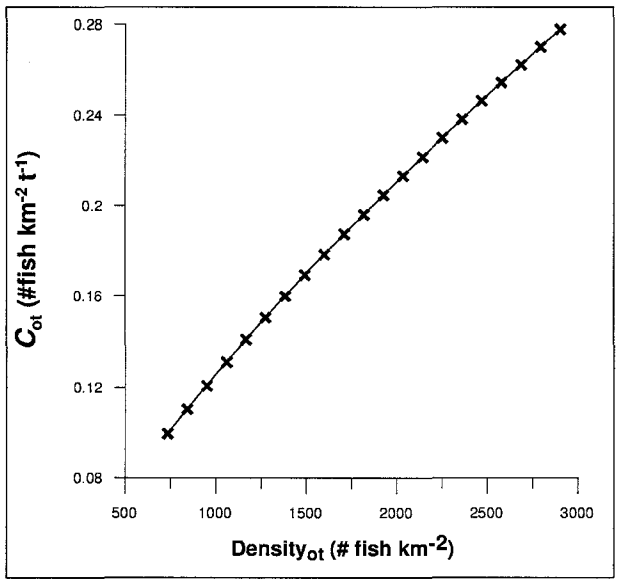


Figure 5.17. Capture rate of other prey, as a function of other prey density.

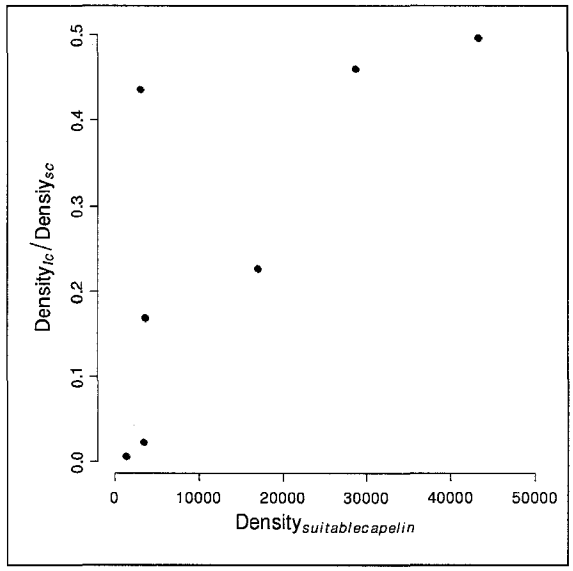


Figure 5.18. Relative density of large capelin, shown as a function of 'suitable' capelin density.

Chapter 6

General Discussion

Animals must consume resources in order to meet their energetic requirements for maintenance, growth and reproduction. However, they do no take these resources in a direct proportion to what they have available in the environment. Foraging theory predicts that animals will choose what resources to consume based on energy profitability.

The function that relates diet to prey availability is a core structural feature of predator-prey models, and plays a central role in determining the outcome of predator-prey interactions, the dynamics of predator and prey populations and their responses to exploitation. Nevertheless, assessments of this function are rare due to the difficulty that studying free-ranging predators imposes on the collection of field data (which implies that its evaluation requires the development of research programs devoted to it) and to the general perception within the scientific community that they are not cost-effective given the characteristic low signal-to-noise ratio of ecological data.

In this Thesis I have tackled this issue by exploring the interaction between the most abundant seabird in the Northern Hemisphere, the common murre, and the focal forage fish of the Northwest Atlantic ecosystem, capelin, as a case study.

The common murre is a specialist seabird that during the breeding season feeds itself and

its chicks almost exclusively capelin. In this study I characterized common murre's diet in terms of three prey categories; small capelin (100-140 mm), large capelin (>140 mm) and other prey (every prey other than capelin). Diet was dominated by capelin (predominating large over small capelin in 3 of the 7 years studied) throughout the study period while the contribution of other prey was almost negligible (Chapter 2).

Furthermore, the common murre did not consume capelin in a direct proportion to what they have available in the environment, rather they take larger capelin to feed their chicks (Chapter 2). This observation agrees with central place foraging predictions, in that they only capture energetically profitable prey thus maximizing the net rate of energy delivery to their offspring.

In order to account for the effects of spatial variability in prey availability and the murre's non-random prey searching behavior, I set up four representations ('scenarios') of the common murre's perception of its prey field according to expected behavior in the light of current knowledge of its foraging ecology (Chapter 4). The scenario that showed the best fit was the Random foraging scenario, which implies that the common murre forages throughout its foraging range and that there is no prey density threshold above which it perceives prey aggregations. This representation of the murre's perception was the most accurate because it reflects the temporal and spatial scales at which the common murre is likely to find capelin aggregations.

Considering this scenario, the prey field (Figure 4.2.) can be schematically characterized in terms of the abundance of suitable capelin as being either high or low.

An interesting pattern that emerges from analyzing diet and prey availability data concurrently is that in the years of high suitable capelin abundance (1997, 1998, and 2004) the consumption of small and large capelin was not significantly different; while the converse is true for the years when suitable capelin abundance was low. I put forth three hypotheses to explain this pattern; during the years in which capelin abundance is high: a) common murres have no difficulty in meeting their energy requirements and hence do not need to select for larger prey, b) their selecting ability is decreased, and/or c) capelin shows a density dependent behavior, *e.g.* diel vertical migration or shoaling behavior may be affected by conspecific density.

The first hypothesis seems to be the most likely explanation for the observed pattern. Central Place Foraging theory predicts that as distance, and hence traveling time, from patch to central place is increased, the greater must be the energy density of the prey selected by the predator (Orians & Pearson 1979). Previous studies have found that when feeding conditions are poor, parental common murres increase their foraging effort thus buffering the chicks against these adverse conditions (Burger & Piatt 1990, Wanless *et al.* 2005). In particular for the common murres breeding on Funk Island, Burke (*in prep.*) observed that in 2005 (low capelin availability) they increased by approximately 50% the mean and maximum foraging ranges compared to 2004 (high capelin availability). Therefore, the murre's prey delivery patterns can be explained within the context of Central Place Foraging Theory (Orians & Pearson 1979); during periods of food shortage they increase foraging effort (travel further from the colony) and, given the high cost of flight for auks (Pennycuick 1987), this would result in greater pressure to deliver larger,

more energetically profitable prey to the offspring.

While 1995 constitutes an exception to the above-mentioned pattern, this year was peculiar in terms of both prey field and diet. In terms of the prey field, it can be characterized as a low-abundance capelin year, and the mean length of capelin was markedly smaller than during the rest of the years considered (Nakashima & Slaney 2001, Carscadden *et al.* 2001b). It was peculiar when it comes to diet in the sense that other prey accounted for more than 30% of the diet, a striking fact considering that the common murre specializes on capelin during the breeding season.

This finding can be framed within the context of ecosystem indicators, an approach that is receiving a lot of attention from the scientific community in the advent of the ecosystem approach to fisheries management (*e.g.* Daan *et al.* 2005). In this context, some ecological characteristics of top predators have been regarded as potential indicators of ecosystem status and performance (Boyd *et al.* 2006). Particular attention has been directed at diets, because this variable is expected to track changes in community structure under the assumption that variations in prey availability are reflected, and most importantly can be effectively detected, in the composition of the diet. This approach seeks to interpret the realized output at the top of the food web without the necessity of understanding the processes that generate and maintain the observed patterns. Although the description and interpretation of patterns is a starting point for understanding the system's dynamics, it can not replace mechanistic understanding since if we do not know why the data conforms to a pattern we can not guess when it will not (Lehman 1986, Levin 1992), nor what the consequences might be. In that sense,

modeling can be a powerful tool for suggesting possible mechanisms and exploring the effects of individual factors on the dynamics of interest (Levin 1992). In this context, the importance of modeling predation interactions is to provide long-term forecasts for events outside those observed previously (Bax 1998).

In this study, I have described the patterns in the common murre's diet and capelin availability, and a pattern that indicates that there's great potential for using the common murre's diet as an indicator of capelin availability emerged from analyzing these two sources of information simultaneously. Furthermore, I also found clear evidence that it is feasible to link common murre's diet and the availability of suitable capelin (*i.e.* >100 mm). This finding opens the door for developing models that can predict suitable capelin status as a function of murre's diet. Building such models would represent a step forward in the development of the indicators approach since it would imply going beyond the description and interpretation of patterns and enabling us to make quantitative predictions about the status of a teleost fish stock from information provided by a top predator's diet. It would also have obvious implications for management; it would contribute to the assessment of capelin status in the Newfoundland area by providing an index of abundance that is easy, quick and inexpensive to obtain. However, before this can be achieved, it will be necessary to link the availability of suitable capelin around Funk Island and the entire stock, which implies assessing the relationship between suitable capelin abundance across different spatial scales (*i.e.*, around Funk Island *vs.* the Newfoundland Shelf) and the link between total capelin and suitable capelin abundance. Since there are no estimates of overall capelin stock abundance in the Newfoundland

shelf for the period considered this linkage remains unknown, but the possibilities implied by the results of this study suggest that this path is worth pursuing. An issue that must be considered when estimating prey availability from measurements of a predator's consumption is that the relationship between these two variables is highly non-linear (Figures 5.10 and 5.11) and plateaus at high prey densities, which means that changes in prey density trigger changes in prey consumption up to a threshold density above which no change in consumption will occur. This can be an important source of uncertainty in the estimation of prey availability (Asseburg *et al.* 2006). However, it doesn't hinder the potential to confidently estimate prey availability up to that threshold density. If such threshold is not too low, this approach could result very informative. A further source of uncertainty in the case of generalist predators is the fact that the precise shape of the relationship between the consumption of a prey and its availability is influenced by the densities of all possible prey species. Notwithstanding, when one prey species dominates in the predator's diet, its monitoring may be an useful source of information on this prey species (Asseburg *et al.* 2006). The relationship between common murre's diet and the availability of 'suitable capelin' is framed in the latter scenario, since the common murre's diet is composed almost exclusively of 'suitable capelin' (Figure 2.2).

Using quantitative models, I have synthesized field data on common murre's diet and prey availability, which provided new insights into the common murre's foraging ecology. For instance, the results of the hybrid model suggest that the common murre only perceives capelin as potential prey, while the occasional consumption of other prey may be a result of murres mistaking it for small capelin. In the same vein, the model that

gave the most interesting insights into the mechanisms that shape the murre's predation process was that derived from functional response theory. The single-species functional responses (subject to the underlying multi-species functional response) of the common murre with respect to its three prey have a hyperbolic shape, which means that as prey density increases the consumption of that prey increases, but does so at a decelerating rate.

Another interest insight gained from the model is that as prey density increases, the prey consumption rate per-capita of prey decreases. This may be the result of several factors; improvement in capelin anti-predator mechanisms with abundance, interspecific competition between parental murres, and/or negative prey switching (prey preference is a decreasing function of the relative density of the prey).

From the perspective of functional response theory, it is interesting that, based on Koen-Alonso's (2007) rationale for classifying multi-species functional responses, I claim that the common murre's functional response is of Type III (*i.e.,* the rate of successful search α_i is a function of prey density). However, if I had followed the classic graphical classification of single-species functional responses, I would have concluded that the functional responses with respect to the three prey are of Type II. This underlines that classifying multi-species functional responses on the basis of the graphical representations of the lower-dimensional single-species functional responses derived from them may be misleading and stresses the need for adopting an explicit quantitative criterion for classifying multi-species functional responses, and within that context shows the importance of performing a meticulous scrutiny of parameter values when working

with functional response models.

In the context of predator-prey theory and the management of marine systems, the contribution of this study is to render a functional form for the relationship between common murre's diet and its prey availability, thus providing us with mechanistic understanding of the processes that underlie the common murre's foraging decisions. This is particularly relevant given that the functional form of models has a profound effect on their outcome and consequently its careful evaluation has been strongly advocated in the ecological literature (Yodzis 1994).

Furthermore, it provides parameter estimates for multi-species models of the Newfoundland marine community that may eventually include common murres (primary capelin seabird consumer of the system) as a component, thus providing some of the elements needed to increase model resolution.

Given the general awareness and recognition among scientists that understanding ecosystem functioning is essential to ensure the sustainable use of marine resources, this study represents a step towards making community ecology the basic science for assessment and advice (Mangel & Levin 2005).

I hope this study will contribute to confuting the belief that finding the link between prey availability and predators' diet in natural settings is not feasible and to encouraging the commitment from scientists and institutions to engage in research dedicated to enhance our understanding of the processes that shape and regulate natural communities.

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Appendices

Appendix A

Common murre's diet composition

Table A.1. Composition of the common murre's parental deliveries, discriminated by year

Year	*Small capelin*	*Large capelin*	*Other prey*
1995	65	45	48
1996	13	56	2
1997	136	137	16
1998	50	37	5
1999	21	36	1
2004	76	74	3
2005	39	65	0
Total	400	450	75

Table A.2. Discrimination of the prey category 'other prey', by year.

Prey species	*1995*	*1996*	*1997*	*1998*	*1999*	*2004*	*Total*
Alligator fish	0	0	0	0	0	1	1
Arctic cod	0	1	3	0	0	0	4
Blenny/rockfish	0	0	2	0	0	1	3
Capelin larvae	0	0	2	0	0	0	2
Gadid	2	0	0	0	0	0	2
Polar cod	2	0	0	0	0	0	2
Ratfish/hake	0	0	2	0	0	0	2
Rockling	0	0	1	0	0	0	1
Sandlance	41	0	1	4	1	1	48
Sculpin	3	1	3	1	0	0	8
Wolf eel	0	0	1	0	0	0	1
Wolffish	0	0	1	0	0	0	1

Appendix B

List of symbols

Table B.1. List of symbols with a brief description and their corresponding dimensions. Note that for those quantities that measurements or estimations were made the units used are provided between brackets.

Symbol	Dimensions	Description
N_i	#prey area^{-1} [km^{-2}]	Prey *i* density
P	#predators area^{-1}	Generic predator density
r_i	#predators (#predators time)$^{-1}$	Generic intrinsic per-capita growth rate
F_i	#prey (#predator time)$^{-1}$	Generic functional response
e_i	dimensionless	Generic assimilation efficiency of species *i*
δ	#deaths (#predators time)$^{-1}$	Generic per-capita death rate of the predator
C_i	#prey time^{-1}	Generic capture rate of prey *i*
h_i	time	Generic handling time for prey *i*
α_i	area time^{-1}	Generic predator's rate of successful search for prey *i*

Table B.1. Continued

Symbol	Dimensions	Description
a_i	area time^{-1}	Generalized Holling MSFR constant coefficient for prey *i*
b_i	dimensionless	Generalized Holling MSFR shape parameter for prey *i*
λ_i	dimensionless	Exponent of the Generalized Holling MSFR
$\%N_{ij}$	dimensionless	Percentage by number of prey *i* in year *j*
$Y_j\{\}$	#prey	Observed parental delivery of bird *j*
y_{ji}	#prey	Number of prey *i* observed in bird *j*
sc	dimensionless	Small capelin
lc	dimensionless	Large capelin
ot	dimensionless	Other prey
π_i	dimensionless	Probability of feeding on prey *i*
$\ln[\mathscr{L}(\boldsymbol{\theta})]$	dimensionless	Log-likelihood
N	dimensionless	Number of observed parental deliveries
$\mathscr{R}$	dimensionless	Likelihood ratio

Table B.1. Continued

Symbol	Dimensions	Description
η_i	dimensionless	Generic linear predictor of generalized linear models
$\beta_{0,i}$	dimensionless	Parameter of the multi-category logit model
$\beta_{m,i}$	area $[km^{-2}]$	Parameter of the multi-category logit model
B_i	dimensionless	Parameter of the hybrid model
$\gamma_{m,i}$	$\{\ln(area^{-1})\}^{-1}$ $[\{\ln(km^{-2})\}^{-1}]$	Parameter of the hybrid model
p_i	dimensionless	Proportion of prey *i* in the diet
AICc	dimensionless	Akaike Information Criterion corrected for sample size
$\Delta AICc_i$	dimensionless	Difference between the AICc of model *i* and that of the best model
n_p	dimensionless	Number of estimated parameters in a given model
φ_{ij}	dimensionless	pairwise relative preference (predator's preference of prey *i* with respect to prey *j*)